A contribution to our knowledge of Arisaema triphyllum

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(WITH PLATES 1–5 AND 70 TEXT FIGURES)

SECTIONAL TOPICS

INTRODUCTORY

Arisaema triphyllum (L.) Schott (TEXT FIG. 1) is one of the most common as well as most widely distributed of the aroids. As such it would seem profitable to give it more attention than has been given. The present work is the result of an attempt to bring together and check up what has been reported, to complete fragmentary parts of reported history, and to call special attention to any features new or unique. It is not the intention to enter into any theoretical discussion, but to present facts as observed. The work has extended over a period of six consecutive

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years. Findings have been checked up by observation of two or more years in nearly every case. Almost three thousand plants have been under observation in the field during this period, and

FIG. 1. A clump of "Jacks" showing general habit. × ⅓ (about).

nearly two thousand plants have been grown in cultures under controlled conditions. The data presented, unless otherwise stated, may be considered as true of plants in Monroe County,

Indiana, and should be compared with those from other sections with due allowance for differences in climatic conditions.

TIME OF DEVELOPMENT OF FLOWERS

That the flower buds of many early blooming perennial herbs are formed during the season preceding their appearance has been long known. In the case of *A. triphyllum* this fact was reported and some structural details given by Foerste in 1883 (10). In another paper, in 1891, Foerste (11) again speaks of the development of the buds of *A. triphyllum* and sets the earliest date for finding of the bud and flower as the "middle of August," for plants growing in the vicinity of Rutland, Vermont.

No description need be given here other than the statement that the flower bud together with the undeveloped leaf or leaves lies (TEXT FIG. 2; PLATE 4, FIG. 56) on the morphological tip of the corm directly under the bases of the season's leaves, and is surrounded by three or more close, sheathing, fleshy scales, the whole forming the terminal bud. In southern Indiana considerable variation is shown in the time of flower bud formation. Specimens collected during the last week of June frequently show flower clusters sufficiently developed for the recognition of individual anthers or ovules. Some specimens collected at this time show sporogenous tissue clearly differentiated. By the first week of August nearly all the plants except those having fruit clusters have withered and died. Examination of corms at this time shows most of the buds well developed. Many ovules show the primary archesporial cell and many anthers, all stages up to well-formed pollen spores. In marked contrast to the conditions just noted, a considerable number of corms examined in late summer show nothing but bud initials, neither leaves nor flower buds being evident. This is equally true of plants which have borne staminate and pistillate flowers during the current season.

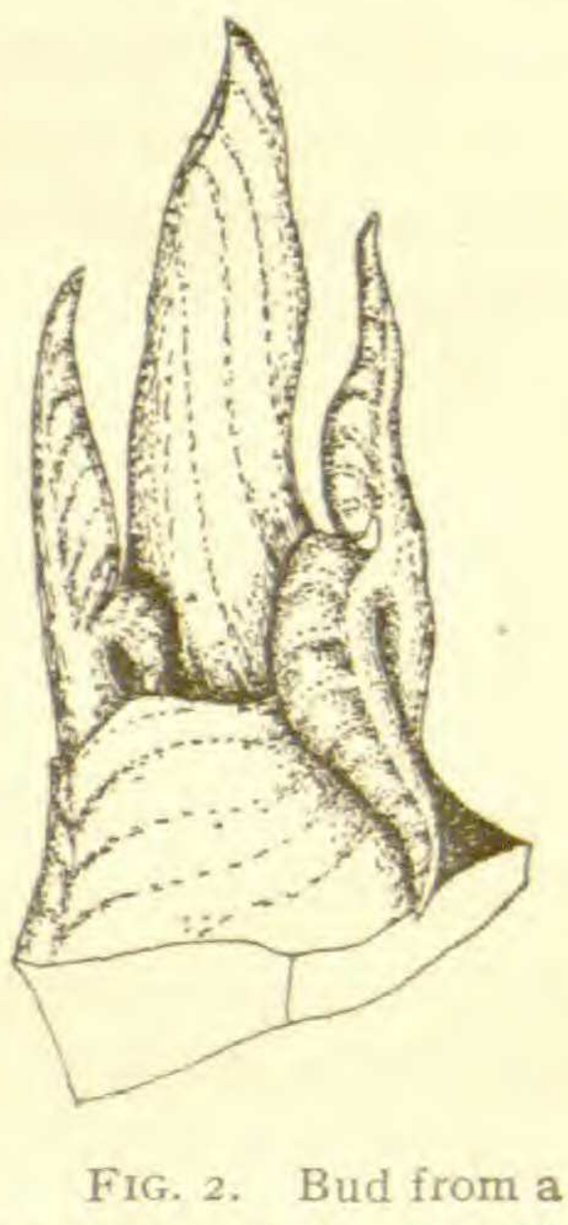


FIG. 2. Bud from a 90 gm. corm, removed August 14. × 3.

Whether or not these plants would bear flowers the following year cannot be determined with certainty; but the finding of an occasional plant in March or early April showing active tetrad divisions indicates the probability that such plants pass the winter with the buds very immature. The wide variations just noted have been observed both in the greenhouse, where all the plants of a group have received identical treatment, and in the field.

Of the accessory floral structures the spathe develops first, and shows the appearance of a miniature but otherwise perfect envelope (TEXT FIG. 2) before the reduction division of the pollen mother cells or the investment of the nucellus by the integuments. With the resumption of activity in the spring the spathe grows rapidly, as a leaf, and is mature before the flower breaks through the soil. The sterile club of the spadix appears as a small conical protuberance above the flower clusters when the individual anthers can first be recognized, and makes its chief growth after the spring development begins. Its mature form is not attained until the flowers are fully developed.

As would be expected from the great difference in the time of development of the flower parts, there is much variation in the time of maturity of the inflorescence. If March be mild and warm, a few "Jacks" may be seen during the first week of April. Most of the plants are in full bloom during the last week of April and the first half of May. A few fresh flower clusters may be found during the first week of June.

It has been observed that the first flowers to appear are staminate. All through the season the staminate spikes are found mature before the pistillate spikes of plants in the same group. Even more striking is the difference in time of maturity of flowers on mixed spikes. On the spikes where the oldest ovule shows a megaspore mother cell with a resting nucleus, anthers with completed tetrads have been found. On older spikes anthers discharging spores have been found with ovules showing tetrads of megaspores or the germination of such.

THE STAMINATE FLOWER AND MICROSPORE

The staminate spike is 5–10 mm. long and its axis 2–4 mm. in thickness, being rather more slender than that of the pistillate

spike. The flowers are contiguous before dehiscence, and sometimes show a somewhat spiral arrangement. Each flower is composed of a nearly sessile group of one to six yellow, purple, or mottled anthers, whose filaments are entirely confluent. The anthers are crescent- or U-shaped. They are usually arranged in pairs with the concave sides together; but in case of odd-numbered groups, this arrangement is lost. In some cases the groups are borne on pedicels as much as 2 mm. long, a condition common among staminate flowers at the top of a pistillate spike (PLATE 4, FIG. 59). In his brief discussion Rowlee (**25**, p. 369) described the filaments as cohering, and the anthers as simple in structure. The meaning of this statement is not quite clear. The writer finds a tendency of the anthers to be two-celled. There are always at least two groups of primary archesporial cells, which in many anthers are confluent long before the pollen mother cells are formed. In other anthers the locules remain distinct almost up to the time of dehiscence (PLATE 2, FIG. 29).

At the time of preparation for the heterotypic division of the pollen mother cells, the sporangium wall is composed of a single epidermal layer and three or four layers of sterile cells. The two outer layers of sterile cells form the wall proper, and the one or two inner layers are clearly differentiated as tapetum. The mature sporangium has a wall composed of an outer layer of epidermis, an inner layer of partly disorganized sterile cells, and between these two, a third layer composed of palisade-like cells with thickened walls (PLATE 2, FIG. 29).

The two divisions of the pollen mother cell are as in the lily. The first division is followed by the formation of a wall before the second begins. All the cells of one locule show about the same stage of development; although the different flowers of one spike may at one time show all stages from resting nuclei to mature pollen spores. In 1899 Atkinson (**2**) studied the details of the reduction division. The writer has nothing to add at this time, as questions of a purely cytological nature are out of the realm of the present work. The second division has not been studied in detail, but an examination of the preparations at hand has shown nothing unusual. As reported by Atkinson (**2**, p. 5) the gametophytic nuclei show sixteen chromosomes. The tetrad is spherical with

the dividing walls in various intersecting planes. Soon after the completion of the second division the spores round off and separate.

The first division of the pollen spore nucleus does not occur until the walls are well formed. The generative cell is isolated by the formation of a delicate wall. The second division occurs just about the time of germination. The mature pollen spores are spherical with an average diameter of 19 microns. Both intine and exine are well developed, the latter being quite firm, without evident pores, and thickly set with short, slender spines.

The germination of the pollen spore and the peculiarities of the pollen tube have been briefly described by Rowlee (25). In the examination of pollen germinated on fresh stigmas, the writer has found that the pollen tubes rarely grow straight but tend to become twisted or folded, although to a less extent than found by Rowlee in the case of spores germinated in an anther cavity. The tube winds about among the outer stigmatic hairs, through the hollow style, and then among the hairs of the inner stigmatic brush before reaching a micropyle.

An interesting point in connection with the pollen spore formation is the appearance of wandering tapetal nuclei, as described by Duggar (9) for *Symplocarpus foetidus*. Just at the beginning of the second tetrad division, the tapetal cells begin to disorganize by dissolving their walls. When the pollen spores begin to round off and separate, nearly all the tapetal cells have lost their walls, and the protoplasm and nuclei have passed out into the mass of spores. The protoplasm appears as a nearly homogenous mass, with faint vacuoles, surrounding the developing spores. The nuclei have enlarged, and become rather densely granular, with distinct nucleoli and vacuoles

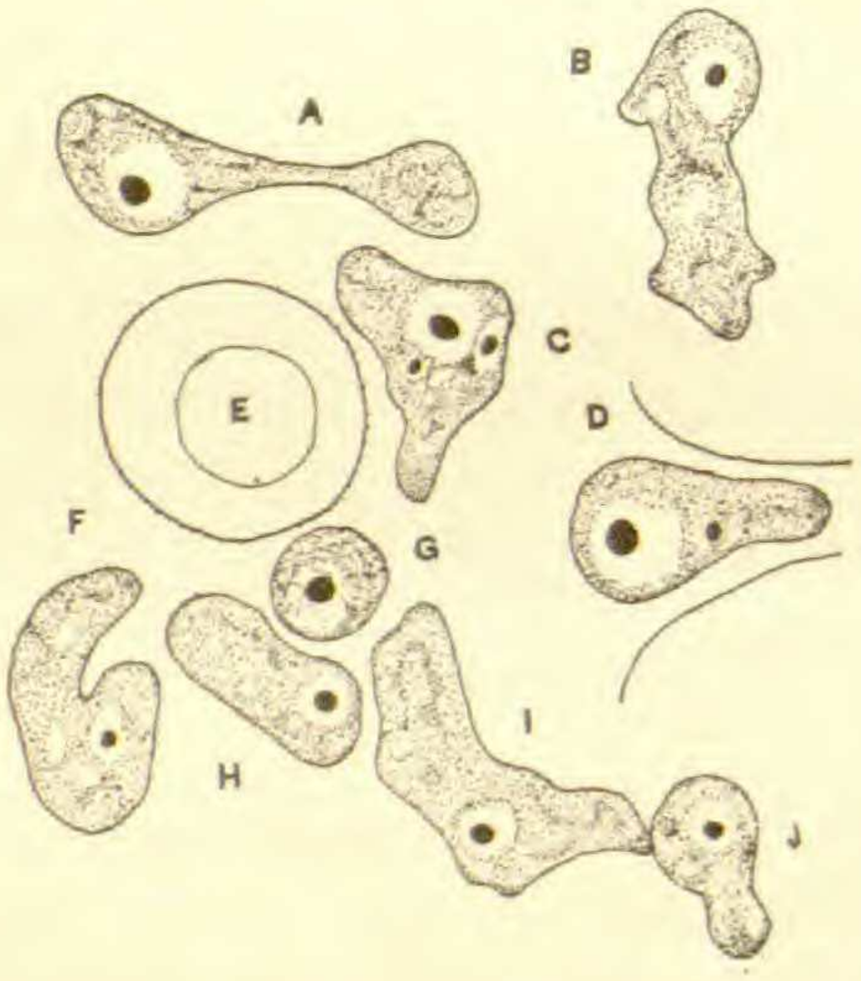


FIG. 3. Migrating tapetal nuclei. × 210. *G*, a quiescent stage common among almost mature pollen spores. *E*, pollen spore drawn for comparison of size. *D*, nucleus from younger locule showing entrance between two tetrads. Other figures show amoeboid forms suggestive of movement.

(TEXT FIG. 3). Whether these nuclei move about in the fluid mass or are carried among the spores by the movement of the protoplasm escaping from the tapetal cells has not been determined, but the forms of the nuclei and their even distribution seem to indicate individual movement. That these free nuclei perform some life function is indicated by their persistence up to the maturity of the pollen spores.

THE PISTILLATE FLOWER

The pistillate flowers arise as broad, contiguous protuberances on the lower portion of the short conical tips of the central axis (TEXT FIG. 4). The development of the ovary wall and the

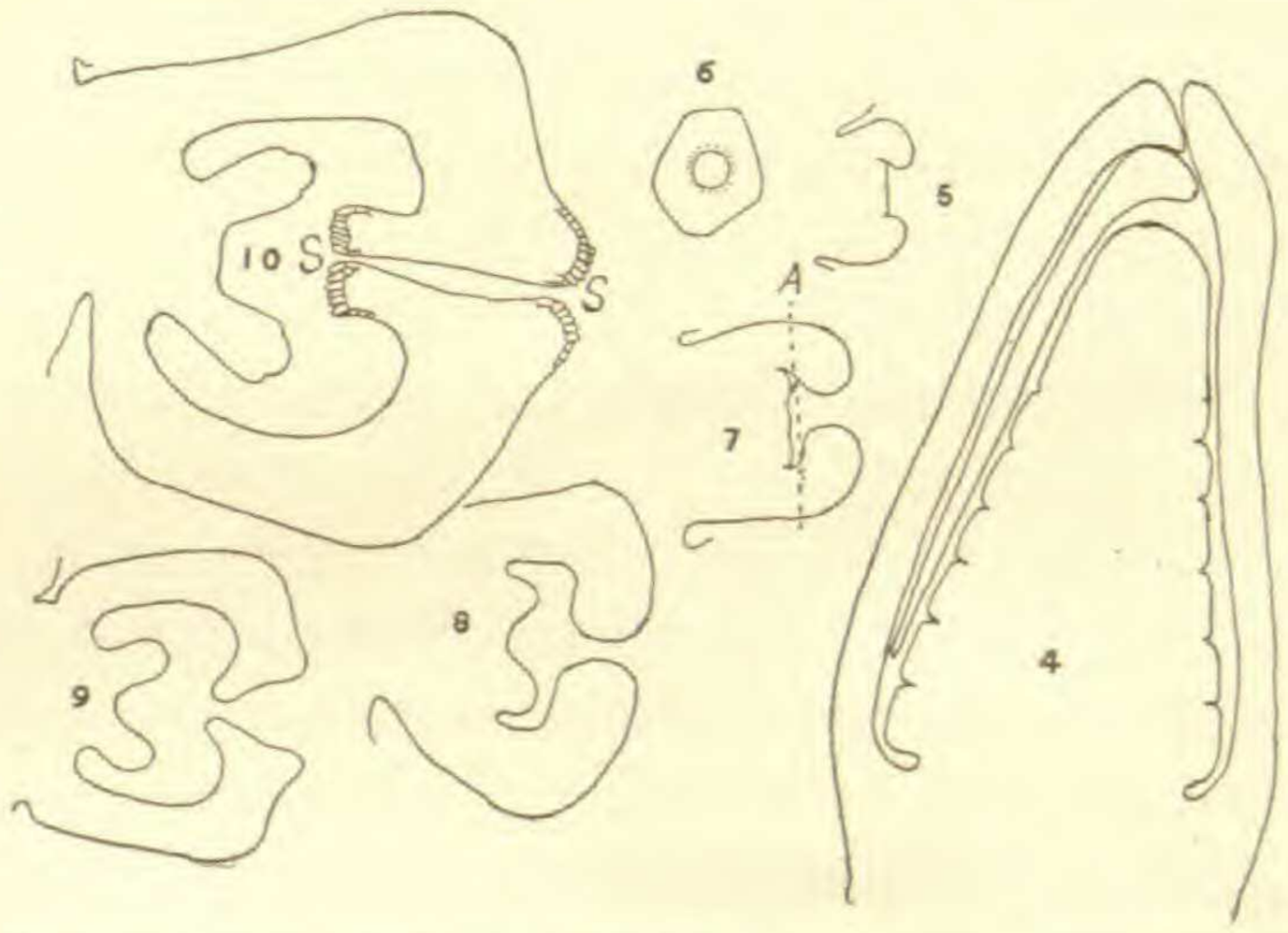


FIG. 4. Longitudinal section of young pistillate spike showing flower fundaments only.

FIGS. 5, 7, 8, 9, 10 show in diagram, successive stages in development of ovary.

FIG. 6 is a cross section of 7 through *A*.

FIG. 10 represents a longitudinal section of an almost mature ovary, showing the beginnings of the stigmatic hairs at *S*. All × 30 (nearly).

beginning of the ovules is shown in TEXT FIGS. 5–10. A section of a mature ovary is shown in PLATE 2, FIG. 33. The one to six orthotropous ovules develop from a small basal placenta. The placenta represents in this case the end of the branch axis, and the ovules, when more than one, seem to be lateral outgrowths. As the ovary wall closes above the cavity the margin is broadened and flattened so that the lower edge closes first, leaving a funnel-like opening (TEXT FIG. 9). Continued growth of the wall and of

the upper edge narrows this opening and so produces a kind of hollow style (TEXT FIG. 10).

About the time the opening in the style reaches its smallest size, the epidermal cells at the upper and lower margins begin to elongate, forming first papilla-like outgrowths (TEXT FIG. 10), and then long, club-shaped hairs (PLATE 2, FIG. 33). Rowlee (**25**) described and figured the stigma of *A. triphyllum*. Briefly stated, the two stigmatic tufts, one inside and one outside the ovary, are similar, being composed of long, club-shaped hairs without septa. The outer hairs of each tuft are the longer, the central ones shorter until in the tube of the style they are mere papillae (PLATE 2, FIG. 26). The hairs of the inner tuft are similar in form, but a few of them become filled with a waxy substance just before maturity (PLATE 2, FIG. 24). These wax cells break down, and the wax, diluted, spreads through the upper part of the ovary, between the ovules and into the micropyles as a thin slime (PLATE 2, FIG. 33). At first glance the presence of this slime might be taken as an adaptation facilitating the passage of the pollen tube from the stigmatic brush to the micropyle. But the fact that cases have been observed where fertilization has taken place without the breaking down of the wax cells or the presence of any slime in the cavity discredits such a theory and leaves the use of the cells a question.

The development of the ovule has been described by the author (**20**), and as it shows no unusual features will be given but brief mention here. Two integuments are formed, the first appearing about the time the archesporial cell is differentiated. When the megaspores are mature the nucellus is entirely invested by the two integuments whose masses of enlarged cells form massive walls about the micropyle. The condition of the integuments about the micropyle is shown in PLATE 2, FIG. 27, almost the same as at the time of maturity.

The mature flower consists of a single ovary attached by a very short stem to the axis of the spadix (PLATE 2, FIG. 33). The ovaries are arranged in a more or less regular spiral order in the spike and are crowded together from the beginning so that they are polygonal in section (PL. 4, FIG. 59; TEXT FIG. 6). The crowded condition continues through the development of the fruit, leaving the berries with flattened sides.

THE EMBRYO-SAC

The development of the embryo-sac of *Arisaema triphyllum* was first studied by Strasburger in 1879 (**26**). Later Mottier (**18**) and Gow (**13**) worked out most of the details in the development of this structure. In 1913 (**20**) the writer reviewed the earlier work and made some additions and corrections. For the sake of continuity the findings of that work will be briefly restated here.

One to four megaspore mother cells are formed independently in the hypodermal layer of the ovule tip. Each of these may produce a tetrad of potential megaspores. One or more of these megaspores may germinate and produce a typical eight-celled embryo-sac. More than one embryo-sac may be formed in each nucellus. The fusion of the polar nuclei is doubtful. The antipodal cells rarely develop fully as in typical angiosperms.

The points of this part of the history worthy of further attention are as follows. As already stated, a regular tetrad of megaspores, variously placed, is formed. Later work has shown that these megaspores are potentially the same, and that even when more than one tetrad is formed many from the plural groups may germinate (PLATE I, FIG. 1). There is no rule of precedence in later development, the matter of quickness of starting and rapidity of growth giving some one spore, as a rule, advantage over the others. One striking example of the precedence of the lowest spore of each of two tetrads has been observed (PLATE I, FIG. 2), but the consideration of this as a regular order is prevented by the many cases where the uppermost or some of the intermediate spores develop into the embryo-sac. That one megaspore usually develops first and at the expense of the others is, of course, indicated by the common formation of but one embryo-sac; while occasional appearance of plural sacs in a nucellus proves the possibility of the growth of more than one spore.

At the time of publishing the earlier paper investigations were under way to determine definitely the action of the polar nuclei and the fate of the antipodal cells. The flowers of another season have been examined since that time, more than two hundred preparations showing approximately mature embryo-sacs having been made. The following seems to be the usual course of events. The two polar nuclei float about for some time in the embryo-sac

cavity, enlarge in size, and finally fuse near the chalazal end. That the nuclei always fuse seems certain from the examination of many preparations showing the nuclei in contact and in partial fusion. The idea is made more certain by the fact that no one of many preparations of past mature but sterile embryo-sacs examined show free polar nuclei. A wide difference in the position of the nuclei at the time of fusion has been noted in a few cases. In one instance the contiguous nuclei were near the micropylar end, and in five cases they were near the middle of the embryo-sac.

After the fusion of the polar nuclei the endosperm nucleus is almost universally found well down in the chalazal end of the cavity, being in some cases almost in contact with the antipodal cells. A remarkable exception was shown by one embryo-sac in which the fusion nucleus was close beside a synergid.

The three antipodal nuclei sink close to the chalazal extremity of the sac, and are soon surrounded by cell walls (PLATE I, FIG. 4). For a very short time they retain their appearance of living cells; but by the time fertilization takes place, they may be seen as shrunken, deeply staining masses pressed close in the chalazal extremity. With the activity of the vegetative nucleus in the residual cavity and the accompanying disorganization of the lower nucellar tissue, the antipodals entirely disappear.

As stated in the former report (**20**, p. 233) a normal egg apparatus (PLATE I, FIG. 5) is formed. Some variations may be worth noting. The synergids sometimes show the principal vacuole above instead of below the nucleus. In some cases (PLATE I, FIG. 3) synergids as large as the egg cell have been observed. A noticeable feature is the frequent occurrence of an egg cell reaching far down into the sac cavity (PLATE I, FIG. 4). In at least one case the egg nucleus was carried to a position near the center of the cavity.

In two preparations from different plants embryo-sacs of mature dimensions were observed, with the primary endosperm nucleus and the shrunken antipodals expected in mature sacs, but showing instead of the normal egg apparatus, the three micropylar nuclei, each inclosed by a mass of protoplasm and a cell wall, floating free in a group in a cell cavity. The similarity of these cells suggests a question as to the primary difference between the synergids and the egg cell and as to what may bring about the final differentiation in the group.

The mature embryo-sac is of the typical monocotyledonous form. It is covered with a cap of nucellar tissue rich in starch, and rests upon a considerable basal mass of the same kind of tissue. Four to eight days may pass between the maturing of the embryo-sac and the withering of the stigma and consequent impossibility of fertilization. During this time the embryo-sac may almost double in size. The greatest change in surrounding tissue to be noted during this time is in the lateral portions of the nucellus. In some cases sacs just mature with fertilized eggs have been found completely invested with a layer of nucellus. In others the last vestiges of lateral nucellus have disappeared before fertilization.

POLLINATION

The pollination of *A. triphyllum* presents a problem which has either escaped the notice of investigators or has baffled attempts at solution. In the case of bisexual spikes where securing pollination would seem to be a simple matter, the staminate flowers mature so long before the pistillate that their pollen is probably inactive when the ovaries are mature. The dioecious character of most of the flowers makes cross pollination necessary. The pollen is slightly adhesive, and being borne deep in the hooded spathe, has practically no chance to be carried by the wind. There are no nectaries or similar structures connected with either staminate or pistillate clusters. In a few spathes insects have been observed eating the stigmatic hairs of pistillate flowers; but this has been observed so few times that the idea of insects coming to the spathes to feed on the stigmatic hairs cannot be entertained. As mentioned in the description of the pistillate flower some of the hairs formed inside the ovary produce a gum which is later reduced to a slimy mass filling the ovary cavity. Whether or not this produces an odor attractive to insects can only be conjectured.

A brief reference to the structure of the two forms of inflorescence will make clearer the observations on insect visitation. The space between the pistillate spike and its spathe (TEXT FIG. 11) is much less than in the case of the staminate spike (TEXT FIG. 12). Such a difference is quite general, although it is not always as great as shown in the figures. In fact, while the staminate spathe may be entered and left again by

small flies and bees without inconvenience or danger, the narrow space around the pistillate spike would make it quite difficult or impossible for the same insects, once in such close quarters, to escape. Observations have proven that many insects find this a veritable death trap.

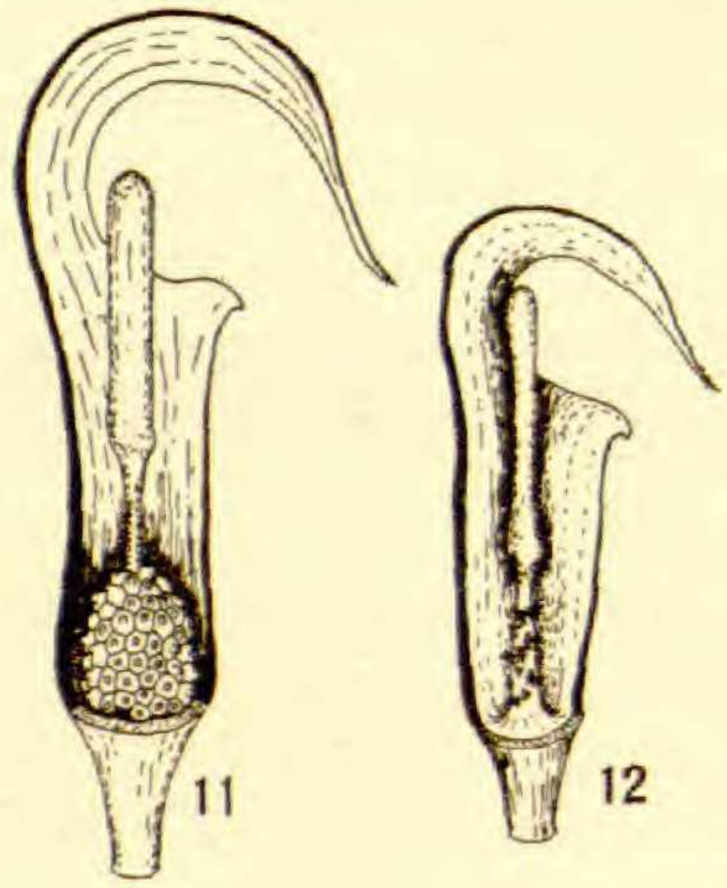


FIG. 11. Longitudinal section through the spathe of a pistillate spike, showing the narrow space about the flower cluster. Reduced about ½.

FIG. 12. Similar section showing comparatively greater space between flowers and spathe wall. Reduced about ½.

With a view of securing some definite basis for a possible explanation of the pollination question, about two thousand plants have been examined and the results with reference to insect visitation tabulated. Different sets of data have been so nearly alike in percentage ratios, that a full account of but one group will be given. From 9–10 A.M. on a bright, warm day, May 18, 100 mature staminate flower clusters and an equal number of mature pistillate clusters were examined. The staminate spathes showed a total of 70 living and 73 dead insects. The pistillate spathes showed a total of 60 living and 557 dead insects. This set of observations could be duplicated many times. The following variations should be noted. In mid-afternoon and early evening few living insects are found in either staminate or pistillate spathes. The greatest number of insects have been found about midday of dark and rainy days. Insects found in staminate spathes are well dusted over with pollen, and many of those found in pistillate spathes also carry pollen on body, wings or legs. The data given above would seem to indicate that the insects seek the spathes for hiding or shelter. Those entering staminate spathes may go out again readily, but carry with them a load of pollen. If the second spathe entered surrounds a pistillate spike, the pollen will probably be left on the stigmas as the insect struggles to escape. This, of course, implies a purely accidental transfer of pollen. The fact that more living insects are found in pistillate spathes than in staminate, as well as the finding of occasional visitors feeding on the stigmas indicates a possible attraction of the pistillate cluster.

Instances like the following strengthen such an idea. In a cluster of plants in the greenhouse one pistillate and twelve staminate clusters were mature at the same time. Examination of these at midday showed 25 living insects in the pistillate spathe and no living insects in any of the others. This is an extreme case, to be sure, but it is not unique.

To summarize the case briefly: It is certain that pollen is carried by insects which seek the spathe, probably for shelter or hiding. The slight space around the pistillate spike insures the transfer of pollen from insect to stigma. There is evidence of insects being attracted to the pistillate flower cluster; but outside of the possible use of the stigma for food or a possible odor from the slime filling the ovary cavity, the cause of such attraction is unknown.

EMBRYOGENY

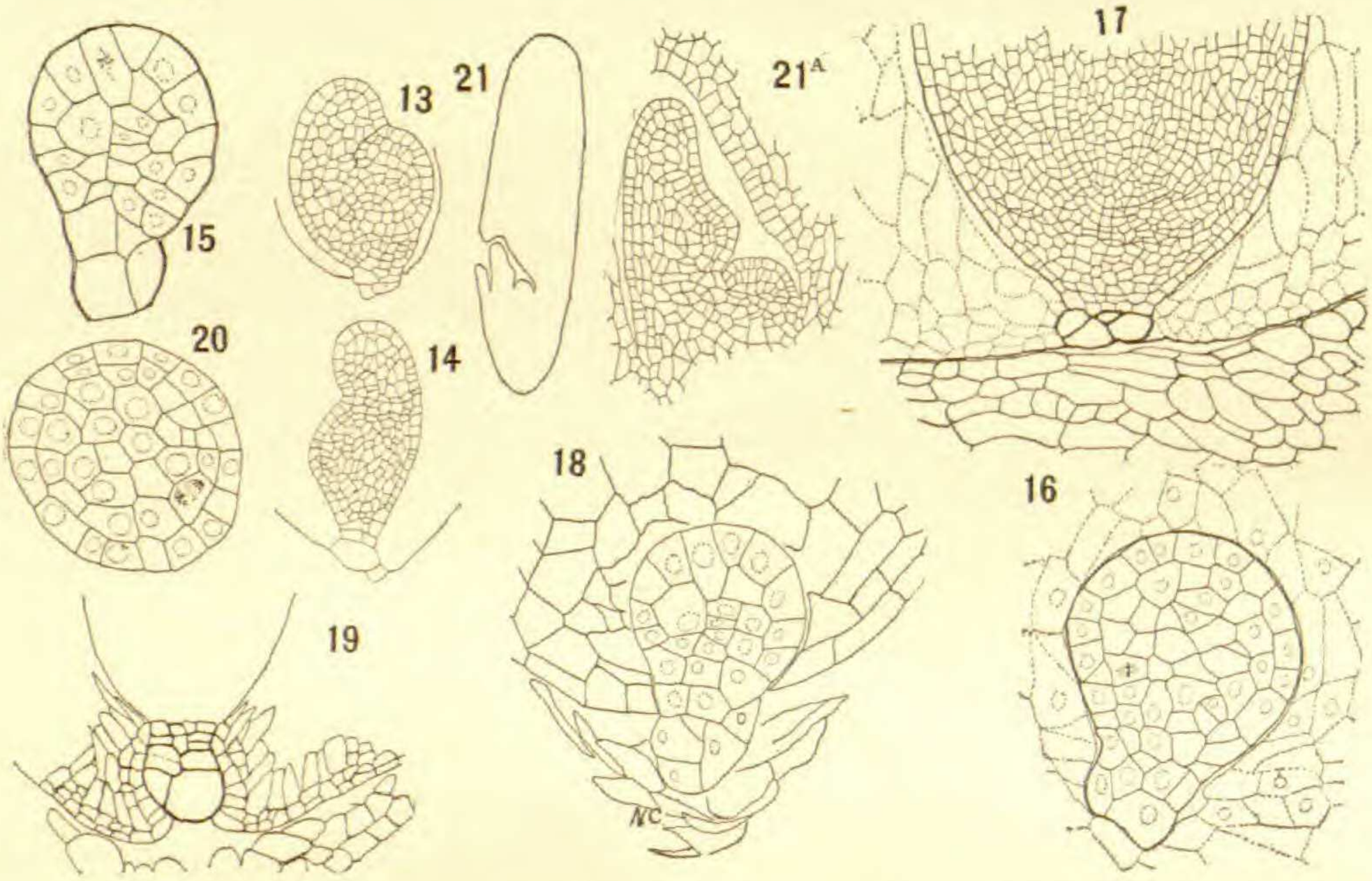
The only published account of the embryogeny of *Arisaema triphyllum* is that by Gow in 1908 (13). The findings of that paper, briefly stated, are as follows: The fertilized egg does not divide until after the endosperm development has begun. The first two divisions are transverse followed by a longitudinal division (13, *f. 20–22*). The figures show a regular chain of two and of three cells, without showing their relation to the basal cell cut off by the true first division.

The following notes are based on the study of more than two hundred preparations covering the phases of development described.

At the time of entrance of the male nucleus, the egg nucleus is well defined and about the size of the synergid nuclei. After fertilization the egg nucleus increases in size so that at the time of segmentation for the first division it has reached about twice its former diameter. This resting stage, if it may be so designated, is about twenty-four hours in length. As reported by Gow (13, p. 42) the fertilized egg does not divide until after the endosperm has well started (PLATE 1, FIG. 9; PLATE 2, FIG. 30). In fact the endosperm mass may be composed of twenty cells before the first division occurs. Ovules fixed 86 hours after pollination show embryos of two to six cells, and endosperm of twenty to forty cells. Those fixed 72 hours after pollination show eggs ready for the first

division and endosperm from the free nucleate stage up to twenty cells.

The first division of the fertilized egg results in the formation of a small embryo cell and a large suspensor cell (PLATE I, FIGS. 7, 11). The suspensor cell may divide at least once immediately (PLATE I, FIGS. 12, 13), and later undergoes several divisions (TEXT FIGS. 13–19). The development of the complex suspensor shown



FIGS. 13, 14. Embryos with two growing regions newly differentiated. The section in FIG. 13 is just a little diagonal. × 65.

FIGS. 13–18. Embryos of increasing age, showing arrangement of cells and development of suspensor. 13, 14, 17, × 65; 15, 16, 18, × 165.

FIG. 18. An embryo with the suspensor group pushed into the broken down nucellar cap, *NC*. × 165.

FIG. 19. An unusually complex suspensor group and an embryo deeply buried in the endosperm. × 65. This and FIG. 17 show the thickening of the suspensor cell walls.

FIG. 20. Cross section of an embryo similar to that in FIG. 16. × 165.

FIG. 21. A diagrammatic longitudinal section of an almost mature embryo. × 15.

FIG. 21*a*. Detail drawing of plumule of FIG. 21. × 65.

does not take place until the embryo has assumed a somewhat globular form, as in TEXT FIG. 15, where two or three divisions have occurred and the resultant cells enlarged. As growth of embryo and endosperm proceeds, the suspensor cells form thick walls, and become closely connected with the aleurone layer of the endo-

sperm (TEXT FIGS. 17, 19). The extension of the suspensor mass beyond the endosperm into the remnant of the nucellar cap with its cells full of starch (TEXT FIGS. 15, 18) suggests a possible function as an absorbing agent. Again a peculiar development has been noted as in TEXT FIG. 19, where the crowding of the surrounding endosperm has forced the embryo, at an early stage, farther than usual from the surface. The embryo has retained its connection with the surface layer, however, by means of a more than usually complex suspensor system. PLATE I, FIG. 8, shows a four-celled embryo and two very short suspensor cells. In the formation of a well-developed suspensor, *Arisaema triphyllum* stands alone among the aroids of which we have full descriptions. *Pistia* with its globular embryo and no suspensor as described by Hegelmeier has been taken as the type of the group. More recently Campbell has described *Lysichiton kamtschatcense* (5) and *Nephthytis liberica* (7) as producing an embryo without suspensors. In speaking of *Anthurium violaceum* Campbell (7, p. 334) says, "the egg . . . is attached by a broad base to the apex of the sac." He also speaks of a rudimentary suspensor formed by the division of the basal segment of the embryo in this species. This seems to be quite similar to *Aglaonema commutatum* as reported by the same author (6), which is said to show the embryo attached to the wall of the embryo-sac by a cell which might be considered a suspensor. Campbell also reports for *Spathicarpa sagittaefolia* the cutting off of a small basal or suspensor cell by the first division of the fertilized egg. In *Arisaema triphyllum*, as already stated, the first division produces two unequal cells, the basal and larger one of which is similar to that cut off by the first division in *Anthurium* and *Aglaonema*. But in *Arisaema* this cell by repeated divisions produces a complex suspensor system.

Returning to the development of the embryo proper, it has been observed that a second and even a third transverse division may take place (PLATE I, FIG. 10). The greater number of the preparations show the second division in a vertical plane, as in PLATE I, FIGS. 13, 14. A second vertical division across the plane of the first produces a four-celled embryo. The four-celled embryo is loosely held together and covers the top of the suspensors as a disk-like cap. The later divisions have not been followed in

detail. Growth takes place by a division of all the cells of the embryo, resulting in the formation of a symmetrical, globular body (TEXT FIGS. 15, 16, 18). TEXT FIG. 20 shows a cross section of such an embryo as is shown in longitudinal section in TEXT FIG. 16. At this stage there is no differentiation other than the formation of a distinct epidermal layer. The form soon changes from globular to ovoid and then tends toward cylindrical. During these changes two growing regions develop. The distal portion develops the cylindrical cotyledon while a lateral protuberance shows the initials of the plumule (TEXT FIGS. 13, 14). The cotyledon continues growth both in length and width much more rapidly than the plumule and finally surrounds the latter almost entirely (TEXT FIG. 23 *B*).

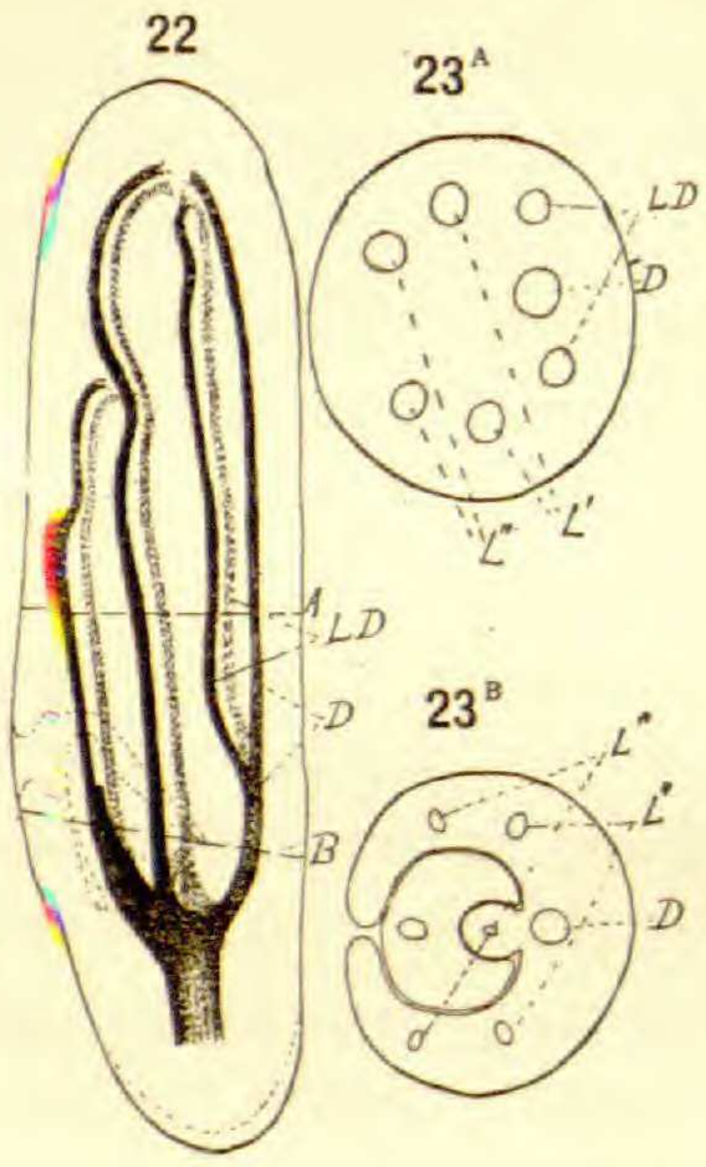


FIG. 22. Reconstructed vascular system for mature embryo. × 20.

FIG. 23*A*. Diagrammatic cross section of FIG. 22 at *A*.

FIG. 23*B*. Diagrammatic cross section of FIG. 22 at *B*. *D*, dorsal strand. *LD*, branches of dorsal strand. *L'*, *L''*, median and forward lateral strands.

The mature embryo is 1–1.5 mm. in length and approximately one fourth as thick. It is cylindrical or ellipsoidal in form, attached to the endosperm periphery by the hardened suspensor cells at the radicle extermity, and lying in a cavity lined by the collapsed endosperm cells from which the food material has been absorbed. It shows clearly marked dermatogen, periblem and plerome areas below the plumule, with a well developed calyptrogen and cap as in a normal root. The plumule shows one leaf enveloping a stem initial group wholly or nearly so (TEXT FIGS. 22, 23*B*). The vascular system of the embryo shows only fundamental elements—largely protophloem, and consists of a cylinder in the radicle with six primary branches just below the plumule (TEXT FIGS. 22, 23*A*). The largest or dorsal strand with two laterals produced at about the level of the plumule tip extends almost to the extreme tip of the cotyledon. There are two lateral pairs of branches, one in the

median lateral region and one in the anterior portion of the sides. All these branches produce short spurs and anastomose rather freely near their distal extremities. The sixth strand, which must be considered the extension of the main axis, passes into the plumule and scale leaf.

The diagram and description given are intended to cover only the more constant features. The differentiation of the parts depends upon the development of the embryo as a whole. In some seeds whose development was cut short by an early drought, but which, none the less, were viable and produced vigorous seedlings, the embryos showed scarcely a trace of vascular strands. In others with long growth period, the primary xylem elements were evident before germination.

THE ENDOSPERM

At the time of the entrance of the pollen tube the embryo-sac contains a normal egg apparatus, three inactive, shrunken antipodals and an endosperm nucleus. This endosperm nucleus, found usually near the chalazal end but sometimes near the middle or even in the micropylar end of the sac, is the most conspicuous nucleus in the cavity. A little before the fusion of the sperm and egg nuclei, the endosperm nucleus divides. Whether or not there is a fusion of one male nucleus with the endosperm nucleus can not be stated positively. Gow (13) states that a second male nucleus enters the embryo-sac and approaches the endosperm nucleus; but he did not observe any fusion or even contact of the two. The writer has not seen any direct proof of such a fusion; but its occurrence is suggested by the fact that division of the endosperm nucleus has been found only at a time shortly after the entrance of the pollen tube into the embryo-sac. This relation is further indicated by the failure of the endosperm nucleus to divide in embryo-sacs untouched by pollen tubes, a fact abundantly proved by the careful examination of numerous sterile ovules beside those developing into normal seeds as well as those from spikes protected from possible pollination. The finding of but six examples of the division of the endosperm nuclei in one bunch of 150 ovules showing stages from mere entrance of the pollen tube up to the formation of the first walls between the free

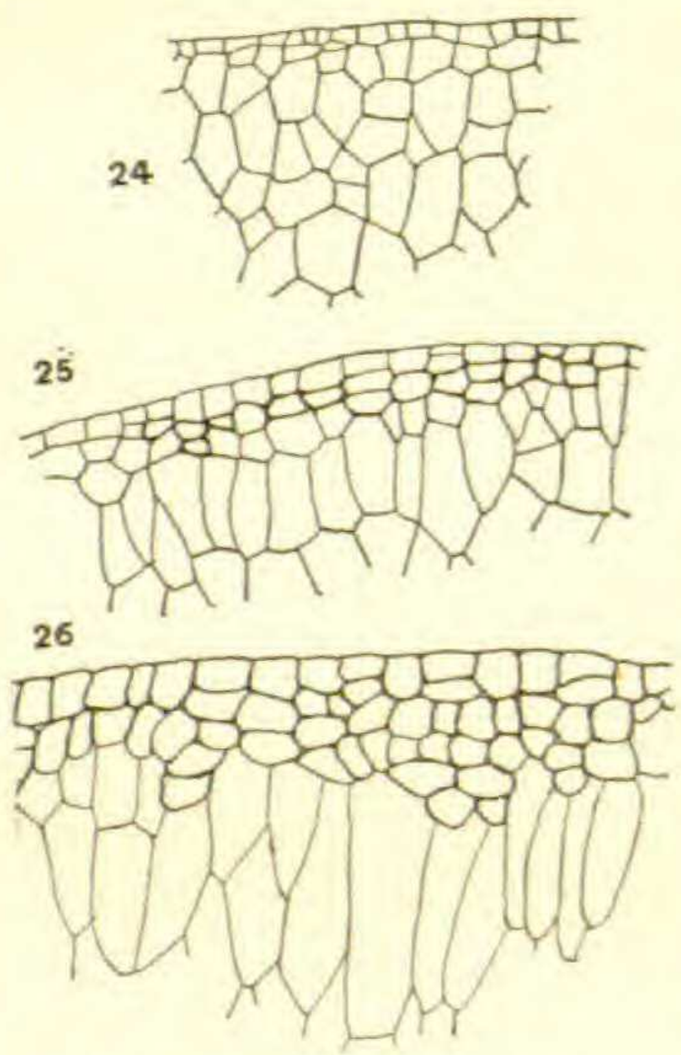
endosperm nuclei, indicates that the division of the primary nucleus and the migration of the daughter nuclei take place very quickly.

At the time of the division of the primary endosperm nucleus, the protoplasm in the embryo-sac becomes highly vacuolated or frothy, many small vacuoles taking the place of the few large ones usually found (PLATE I, FIG. 6). Some preparations seem to show a delicate cross wall formed after the first division of the endosperm nucleus. Most of the preparations seem to indicate that nothing more than a slight condensation of the protoplasm occurs. It seems certain that one daughter of the endosperm nucleus moves toward the egg and by two or three consecutive divisions produces four to eight free nuclei in the upper portion of the embryo-sac, PLATE I, FIG. 6. Contrary to the report of Gow (13, p. 42) these nuclei do not retire to the periphery of the cavity but remain scattered promiscuously through its upper portion. There is a slight tendency for all to move toward the micropylar end of the sac, so that the mass of large irregular endosperm cells, produced by the formation of walls in all directions about the nuclei, is crowded into that portion of the cavity (PLATE I, FIGS. 7, 9, 12). Congregation in the upper end is further produced by the rapid increase of liquid contents in the lower or residual cavity. The embryo-sac enlarges rapidly at the time of fertilization and the remnant of the lateral nucellar tissue is quickly disorganized. As a result, not infrequently the nuclei of this tissue are seen in contact with the thin walls of the new endosperm cells or even buried in the protoplasm of the cavity before walls are formed, so as to seem to belong to the endosperm. At this early stage, however, the active endosperm nuclei are quite large and well organized, frequently showing two or more nucleoli. In older cells the nuclei are smaller and resemble those of the nucellar tissue closely enough to be confused with them.

The formation of the endosperm as just described leaves the egg cell (and the synergids if not destroyed) closely invested by the upper end of a large endosperm cell (PLATE I, FIG. 9) or by two or three such cells (PLATE I, FIGS. 7, 11, 14). For a time further growth of the endosperm is accomplished by the division of the cells bordering the first wall formed across the embryo-sac cavity.

Here a well-defined plate is soon formed (PLATE 1, FIG. 7; PLATE 2, FIG. 30). These lower cells continue to divide and grow, pushing the mass into the lower cavity. The pressure of the liquid contents of this cavity opposes the encroaching mass and causes its dome-like form. Growth of the whole mass of endosperm continues, more rapidly near the lower margins, less rapidly in the central portion, until the residual cavity is surrounded except at the chalazal end where the base of the nucellus and the adjoining integumentary tissue has been broken down. Soon after a definite plate of endosperm has been formed next to the residual cavity, there is developed a region of specially active tissue two or three cells above the lower surface of this plate (PLATE 2, FIG. 25). By the active multiplication and growth of the cells in this region the plate is forced downward into the residual cavity, and the mass of endosperm is increased. By the same action the cells of the endosperm bordering the residual cavity are subjected to lateral pressure between the restraining walls of the integuments until they become long, narrow and palisade like. During this time the large cells first formed have divided until they have surrounded the embryo with small, compact cells in every way similar to those composing the mass of the endosperm.

When the endosperm mass is about one third formed there appears a peripheral layer of cells unlike those of the body of endosperm. By periclinal division of these an irregular layer of short flat cells is formed, varying abruptly from one to five cells in thickness. TEXT FIGS. 24–26 show consecutive steps in the development of this layer. These cells are ultimately filled with protein food stuff, probably aleurone. In the mature seed the endosperm cells, except the aleurone layer, are filled with starch in the form of small simple and compound grains. The process begins in the peripheral cells of the upper portion and extends downward



FIGS. 24–26. Three stages in the development of the peripheral proteid-bearing layer of the endosperm. FIG. 26 was drawn from a section of almost mature endosperm. All, × 52.

and towards the center. A cylindrical portion immediately below the embryo is the last to befilled. The cells about the embryo lose their starch to the growing embryo and remain as a mass of crushed cell walls.

The characteristic feature of *Arisaema* among the aroids is the segregation and the sterility of one daughter of the primary endosperm nucleus and the migration of the active endosperm nuclei to the micropylar portion of the embryo-sac cavity. The formation of a few free nuclei followed by the formation of walls simultaneously between these occurs in *Lysichiton kamtschatcense* (4), but in that case the walls extend entirely across the cavity instead of breaking it up into irregular cells; and the whole cavity is divided up by these cross walls instead of a rather small micropylar portion as in *Arisaema*. The formation and persistence for a time of large endosperm cells in the micropylar extremity of the cavity has been noted in *Lysichiton* (4) and in *Aglaonema commutatum* (6). Along with the other forms, there is in *Arisaema* no migration of the free endosperm nuclei to the peripheral layer of protoplasm.

THE RESIDUAL CAVITY

As noted elsewhere the formation of endosperm in the upper portion of the embryo-sac leaves in the basal portion a large cavity, which may be designated as the residual cell or cavity (PLATE 2, FIG. 31). This cavity contains a lining layer of protoplasm, abundant cell sap and a daughter of the primary endosperm nucleus. The nucleus is the most conspicuous feature of the cavity, having the appearance of a large resting vegetative nucleus with a well defined nuclear membrane and a conspicuous nucleolus within the vacuolate nuclear sap (PLATE 2, FIG. 32). Before definite marks of decomposition appear, this nucleus may reach a diameter of 100–110 microns, and its nucleolus a diameter of 20–25 microns. Later the nucleolus divides or fragments first into a few and then into many small portions. Soon the nuclear cavity shows a more marked network of fine threads and by the time the endosperm has reached half its mature mass, the outline of the greatly enlarged nucleus becomes irregular, the nucleolar fragments disappear and only a mass of fine fibrils remain in the cavity. The enlargement and disintegration continue as the seed matures until the nucleus

may fill a fourth or more of the residual cavity before finally becoming indistinguishable from the remnants of protoplasm around it.

Immediately after the organization of this vegetative nucleus, numerous leucoplasts appear in the residual cavity. They are found chiefly clustered closely around the large nucleus, which they sometimes completely envelop with their own mass and that of the starch they form. The basal nucellar tissue is being rapidly broken down at this time, and the starch stored in the inner integument is being withdrawn. It seems to be the business of this vegetative nucleus and the accompanying leucoplasts to elaborate the food secured from surrounding tissues for absorption by the growing endosperm, or in the case of over supply, to reorganize it into stable starch form. Even after the disorganization of the nucleus the leucoplasts seem active. They are the last organized bodies to disappear from the residual cavity, and may be observed singly or in globular masses of the size of a normal endosperm nucleus after the large nucleus of the cavity has completely broken down.

A point of special interest to the writer is the fact that in ovules having no fecundated egg, the primary endosperm nucleus behaves much as the nucleus just described. The leucoplasts congregate about it and often almost fill the embryo-sac with masses of starch grains before the general decline of the tissues begins.

The activity of the vegetative nucleus is accompanied by a marked increase in the size of the residual cavity. It not only occupies the place of the disintegrated antipodal cells and basal nucellar tissue, but it crushes the inner integument from which the food material has been removed. Finally by the pressure of its increasing liquid contents it forces the endosperm toward the micropyle, and spreads the base of the ovule, giving it the characteristic form of the seed (PLATE 2, FIG. 31).

THE SEED COATS

In order to understand fully the steps in the development of the seed coats, a statement of some nutritive processes preceding fertilization is necessary. During the tetrad divisions and the maturing of the megaspores, the cells of the nucellus become filled with starch. During the growth of the embryo-sac all this starch

is withdrawn from the lateral portions and much from the basal portion of the nucellus. From the maturity of the embryo-sac to the time of fertilization starch is rapidly stored in the integuments, except in their upper portions. Both the integuments become considerably thickened, and the inner one shows a peculiar elongation of the cells bordering the basal portion of the embryo-sac and nucellus (PLATE 2, FIG. 28). A like increase in size of the cells of the basal nucellar tissue is also noticeable at this time (PLATE 2, FIG. 27). These cells, as well as those of the integuments, become well filled with starch, especially if fertilization does not take place until late. The changes so far noted are not in any way the result of stimuli connected with pollination or fertilization, as is shown by the fact that they occur to a noticeable extent in ovules of flowers protected from possible pollination, and in ovules which have failed to develop any embryo-sac, as is the case shown in PLATE 2, FIG. 27.

After fertilization has taken place the thickening of the integuments and the accompanying gathering of the starch continue for some time. As is described in connection with the history of the endosperm, very shortly after the organization of the vegetative nucleus in the residual cavity, the basal nucellar mass is destroyed. The subsequent increase in the size of the whole embryo-sac cavity is due to pressure of rapidly increasing cell sap. At the same time the food from the integuments is transferred to the residual cavity and thence to the endosperm and embryo. As a result of this expansion and food transfer the inner integument is reduced to a sheath of dead empty cells, crushed against the outer integument. The food is withdrawn from the second integument by way of the chalaza, and the inner cells crushed. Before this is accomplished the four outer layers of cells form thick cutinized walls (TEXT FIG. 27), and so produce a firm outer covering of the seed. Many of the cells of the outer integument become filled with a tannin compound, which Rennert (**22**) has noted as a preservative measure at the time of germination. The cell walls of the integuments persist so that the mature seed is sur-

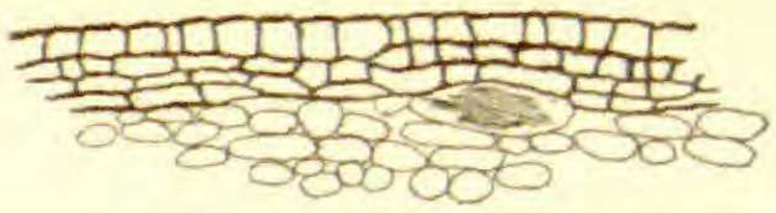


FIG. 27. Epidermis and underlying cells with thick walls forming the outer part of the testa. × 52.

rounded by two distinct coats. The necks of the integuments shrink and remain as a beak over the micropyle of the seed. With the drying of the funiculus and contiguous structures the basal walls cover the remains of the residual cavity whose presence is indicated by a more or less marked depression at the base of the mature seed.

THE FRUIT

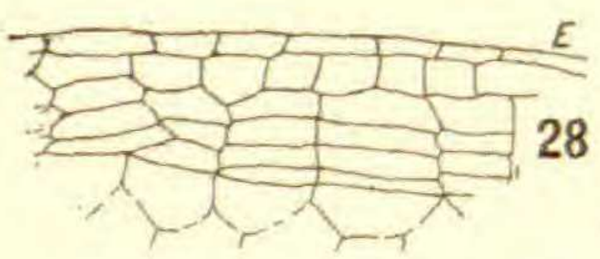
The wall of the ovary is composed of a definite epidermal layer with thickened and somewhat cuticularized walls, and an inner or lining layer of thin-walled cells. Between these layers in young ovaries is a loose mass of spongy tissue composed of nearly isodiametric cells. These spongy tissue cells elongate along some one axis in various directions and so produce large intercellular spaces. This formation is less evident next to the epidermis where one to three layers of cells retain their earlier form and position. In the upper part of the ovary the air spaces are largest, which, together with the formation of many large raphide cells, makes this portion of the wall much thicker than elsewhere (PLATE 2, FIGS. 26, 33; TEXT FIG. 51). As the seeds mature the growth of the ovary wall continues so that a considerable space is formed for the growth of the seed (PLATE 1, FIGS. 17, 20). At this time the chloroplasts break down and irregular, more or less globular masses of yellow bodies appear in the formerly chlorophyll-bearing cells, giving the fruit its characteristic color.

The mature fruit is a scarlet or vermillion berry 3–6 mm. in diameter, with flattened sides and containing one to six white seeds (PLATE 1, FIGS. 15, 16, 18). As the fruits mature, the axis of the spike elongates and enlarges by increase of its air spaces so that the fruits are not more closely crowded than the ovaries at anthesis (PLATE 1, FIGS. 20, 21). The clusters of scarlet or vermillion berries are among the most conspicuous of late summer fruits and are carried by birds, mice, and chipmunks. The use of the fruit pulp as food by animals is made more possible by the development of a slightly sweet taste and the disappearance of most of the raphides from the thoroughly ripened pulp.

DEVELOPMENT AND LIFE OF THE CORM

In a brief paper before the regular winter meeting of the Indiana Academy of Science in 1912 (19) the writer suggested that the life of the corms of *A. triphyllum* was fairly definitely fixed, no part of the corm probably being more than four years old. Wider observations of mature corms along with a study of the development of corms in seedlings makes it possible to add materially to the report cited.

MacDougal (17) and Rennert (22) have given quite full accounts of the germination of seeds of *A. triphyllum* and *A. Dracontium* and the development of the seedlings. The author has verified the findings set forth in the two papers mentioned, with some minor exceptions to be noted below. The findings of MacDougal and Rennert for *A. triphyllum* may be briefly summarized as follows: In the presence of moisture and suitable temperature the seeds swell, and the outer rows of testa cells are dissolved. The starchy endosperm, protected from external agents by the tannin impregnated cellulose layer of the testa, is dissolved by diastase formed by the epithelium of the imbedded embryo. Within the embryo the cotyledon elongates by a lengthening of its cells and pushes the hypocotyl and plumule bud from the seed. By a curvature of the cotyledon just outside the seed its point is directed downward. The hypocotyl enlarges as a result of the increase in size and number of its cells. By active division of the procambium cells both in their longitudinal and transverse diameters much new tissue is rapidly formed. The fibro-vascular system, raphide cells and storage cells are soon differentiated, while a layer of periderm (TEXT FIG. 28) consisting of five or six layers of empty flattened cells arises on the outside of the enlarged portion and finally separates the newly formed corm from the cotyledon. While these changes have been



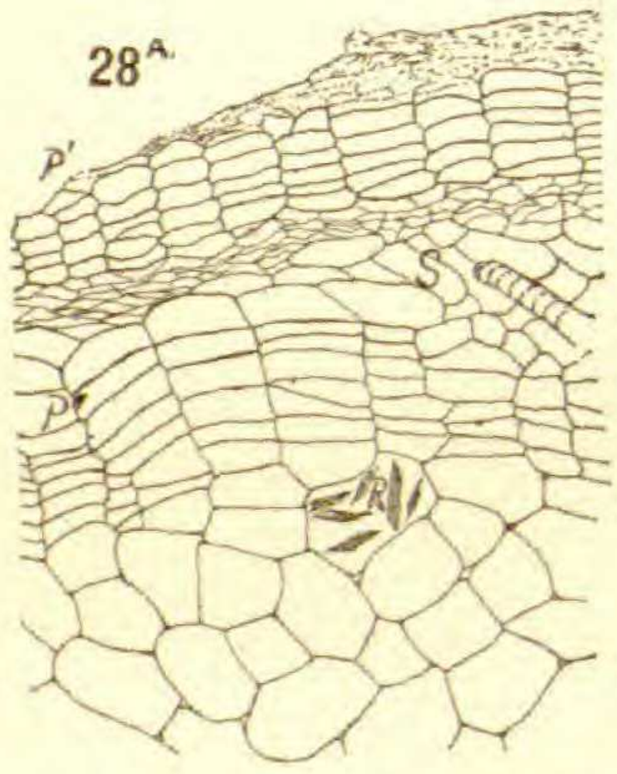
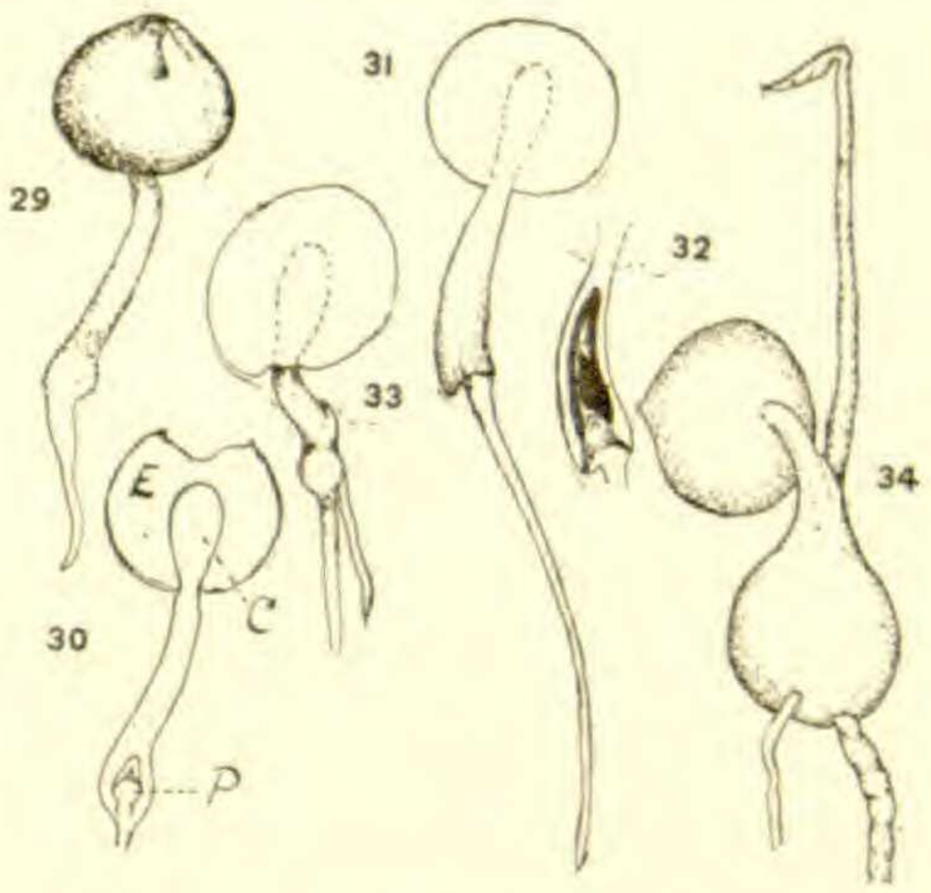


FIG. 28. The phelloderm layer forming beneath the epidermis, *E*, of a first year corm. × 60.

FIG. 28*a*. An old layer of phelloderm, *P'*, and a new layer, *P''*, forming within and cutting off the exhausted starch cells, *S*. *R*, a raphide cell. × 60.

taking place, growth and development of the parts of the plumule has taken place. The first leaf with its blade closely convolute and bent forward is pushed up by the rapidly elongating petiole (PLATE 3, FIG. 34). Without going into greater detail, it has been found that first a primary root arises at the tip of the hypocotyl before any considerable enlargement has taken place, and later one to three other roots appear at various points on the lower half of the young corm. The structure and activities of these roots will be considered in a separate section. TEXT FIGS. 29–34 give the gross structure and the changes during germination. FIGS. 34–39 (PLATE 3) show the development of the seedling leaf.



FIGS. 29–34. Germination of seed. × 2.

FIG. 30. A longitudinal section of seedling in FIG. 29, showing one end of the cotyledon, *C*, in the endosperm, *E*, and the other carrying the plumule, *P*, into the soil.

FIG. 31. A later stage,—section of part of seedling in FIG. 31, showing advanced plumule and the origin of the secondary roots.

The papers cited leave the impression that a primary difference between the germination of *A. triphyllum* and *A. Dracontium* is in the fact that most seeds of the latter germinate blindly, i. e., without producing functional plumules the first season, while the seeds of the former universally produce functional plumules the first season. During three years the author has grown many *A. triphyllum* seedlings and has always found a considerable number of blind germinations. The following data from one season's cultures will explain. Seeds were freed from the fruit pulp and planted in good moist loam in 20 cm. flower pots and given as nearly ideal conditions as possible. Careful record was made of all leaves appearing above ground during the growing season, and after all leaves were dead the corms were removed and counted.

Seeds planted	900
Leaves above ground	643
Corms removed	767

Difference, indicating number of blind germinations, 124, or 16 per cent.

This result has been repeated with slight variations during the three seasons. Cultures kept in the greenhouse from the time of planting, those allowed to freeze sharply two or three times and then brought into the greenhouse, and others allowed to remain outside during the entire winter all showed about the same ratio of percentage of seeds producing functional plumules and of those germinating blindly. These findings have been further strengthened by the discovery, in cultures of *A. triphyllum*, of corms without plumules, very similar to those of *A. Dracontium* during the growing season.

Briefly stated, *A. triphyllum* seeds produce during the first season underground stems or corms in which is stored the transformed food from the endosperm in the case of those germinating "blind," and in addition to this food, that which is produced by photosynthesis in the first leaf in the case of those producing functional plumules. At the end of the first growing season the corms, surrounded by a layer of periderm, surmounted by a single terminal bud, and entirely free from roots and seed remnants, have much the appearance of well nourished mature plants except in size. The largest corms found were in cultures with a total growth period of fifteen weeks. They were 15 mm. long and 12 mm. thick. The range of size in the corms of these cultures was from 5–12 mm. in thickness and 6–15 mm. in length, with the exception of a few which were about the size of seeds. The number of these small corms was so nearly that of blind germinations in each culture that a relation between the two is certainly suggested. FIGS. 61, 62 (PLATE 4) are from photographs of two such groups of corms. FIG. 61 probably represents the blind or incomplete germinations and FIG. 62 a part of the complete germinations from seeds of one planting.

Some data concerning conditions for germination, not given by previous investigators, may well be given here. Seeds freed from the pulp were planted 2 cm. deep in rich loam in flower pots on November 16. These cultures were divided into three groups, *A*, *B*, *C*, and subjected to different conditions as follows:

A. These cultures were left in the greenhouse at an average temperature of 70° F. from the time of planting. The first leaves appeared above the soil January 15. The last leaves to appear

were noted March 26. Thus the total period of germination covered nearly ten weeks. The total number of germinations was 86.6 per cent. of the number of seeds planted, and 20 per cent. of germinations were blind.

B. These cultures were put outside until March 13 with the pots buried level with the surface of the soil. They were removed on March 13 to the greenhouse with an average temperature of 70° F. The first leaves appeared April 3, and the last ones April 23, showing a germination period of twenty days. The number of germinations was 87 per cent. of that of the seeds planted, and of the germinations 19 per cent. were blind.

C. These cultures were left in the greenhouse lobby at an average temperature of 50° F. until March 12, when they were placed in the greenhouse beside cultures *A* and *B*. The first leaves had appeared March 6, and the last ones appeared April 23, thus giving a germination period of seven weeks, and a total germination of 82 per cent., 8.1 per cent. of which were blind.

At this time it is desired to call attention to but three evident facts indicated by these germination tests, namely: that there is a considerable variation in the length of the quiescent period required by different seeds of this plant; that this period may be lengthened and the total germination period of a group shortened by repressing early germinating seeds through low temperature; and that the exposure of seeds to frost or freezing does not materially increase the total germination percentage or the percentage of blind germinations.

Cultures have been made by using corms one, two, and three years old and subjected to conditions similar to those described for cultures from seeds. In general, the temperature differences produced no effect other than to lengthen the dormant period when at or below 50° F. Corms have not been induced to begin growth before the first week in March, and but few before the last of March, with some notable exceptions now to be given.

A group of one year corms was planted in the usual way on June 24, kept moist and left in a room with a temperature range from 55° to 80°. On July 11 a part of these corms had pushed normal trifoliate leaves above the soil. These grew until the middle of September. The corms were removed on October 31,

while they could yet be identified by the dead leaves, and replanted in another pot and left with other cultures in the greenhouse lobby until the following April 3, when all were removed to the main room of the greenhouse. At this time a leaf had appeared. By June 3 all these corms had produced leaves equal in size and vigor to the usual third year plants. These plants will, of course, be closely watched to determine whether they will remain true to their double annual growth.

After the leaves had died down at the end of the first season of growth, the corms were collected, grouped according to size and replanted in pots of rich loam. During the second season of growth the familiar trifoliate leaves were produced. Examination at intervals of a few days showed the following changes in the corms. With signs of growth about the bud,—lengthening of the investing scales and the appearance of roots about their bases,—the lower portion of the starchy tissue began to soften. In five to ten days the starch had been dissolved by an enzyme, and two weeks later only a dry hull of investing periderm remained, the dissolved food material having been entirely absorbed. About one fourth of the fleshy part of the corm was used up in the growth period. See FIG. 48 (PLATE 3) for the portion absorbed by an older corm. Microscopical examination at the beginning of this change showed a layer of phellogenous cells (TEXT FIG. 28 *a*) formed through the food reservoir and cutting off the portion in which digestion was taking place. This new tissue covered the remainder with a close coat up to the base of the bud, leaving only passage for the absorbing vascular strands. At the end of the growing season the corms showed a new, large and well-developed terminal bud covered with the dry shreds of the dead leaf base. The basal part was covered with the wrinkled first periderm. Just at the basal margin of the bud scales were one to three lateral buds. A few of the smallest corms lacked these buds entirely. Just on a level with the ring of lateral buds was a ring of readily noticeable scars where the roots had been attached (PLATE 3, FIG. 49). In size the corms measured 6–15 mm. in length and 3–10 mm. in thickness. This growth had occurred in two directions, longitudinally and radially about the long axis, and had been accomplished by the production of new storage tissue just beneath the terminal bud.

Growth during the third and fourth seasons is not marked by any peculiarity. The corms increase in size because of additional storage of starch, and new lateral buds are produced each season (PLATE 3, FIG. 49). At the end of the fourth season of growth the largest corms show spikes of staminate flowers. Such corms measure 15 mm. or more in thickness. Of the plants grown from seed by the writer only about 10 per cent. produced flowers the fourth year, the remainder failing to produce flowers before the fifth or sixth year.

After the first appearance of the flowers the growth and activity of the corm is quite regular, there being new lateral buds formed (PLATE 3, FIG. 49) as before and new food material stored up each growing season. The increase in size is not uniform from year to year, for, while constantly increasing amounts of food are removed from the corm each year for use in producing leaves and flowers, the amount of new storage is always dependent upon the length of the season of growth. So after several consecutive short growing seasons some old corms may be greatly reduced in size as a result of the drain to produce early growth and the failure to replace the food so used. The mass of starch is not divided into sections as it is stored up, but the dividing layer of phelloderm is formed each year, cutting off the portion to be used at that time. In the case of several consecutive poor growing seasons the available amount of food becomes so reduced that growth of leaves and flowers is curtailed, and the production of flowers may even be entirely suspended. In the majority of cases examined in the field, the appearance of buds and root scars seems to indicate that the oldest portion of the corm is four years old or thereabout.

Another point worthy of note is that a small number of the corms, 3–5 per cent., lie dormant during whole growing seasons. This is true with corms of all ages from one year up. As yet no reason for this phenomenon has been suggested. Neither is there apparent any regularity to indicate a cyclic occurrence of resting periods. It has been noted, however, that in a very few cases the resting period covers only a part of the season, and, consequently, the plants appear in late summer. This is probably related to the phenomenon of double seasonal growth mentioned above.

The formation of lateral buds has already been mentioned.

These vary both as to number and size. Usually not more than three buds are formed in a season. The size varies with the size of the primary corm, and with the length of the growing season. As stated above, the buds appear first with the growth of the second season. They may then be as much as 2 mm. thick or may be indicated merely by a slight hump over the bud initials. Mature corms may produce buds varying from initial cell groups up to bodies as large as third year seedling corms, i. e., up to 15 mm. in thickness. The greater part of the growth is made the first season. In some cases growth is noticeable after the first season. The buds may be broken from the primary corm and begin independent growth at any time after their formation; and they are regularly pushed off with the dead periderm about the fourth year. Very rarely they produce roots and begin independent growth while attached to the old corm (PLATE 5, FIG. 69). But in no case has the writer seen a bud shrivelled as would be the case if any of the starch should be at any time withdrawn into the parent corm. After being detached the buds develop in every way as seedling corms, and require one to several years of growth before producing flowers. Gow (14, p. 135) states that buds may produce flowers the season following detachment; but the writer has failed to verify the finding.

It will be seen at once that, since they may be readily broken off by trampling of animals or by soil movements resulting from freezing or floods, these buds are important means of vegetative propagation. In fact, the increase in number of plants where large corms have been dug up, the spreading colonies of small plants in wooded pastures, and finally, the very few seedlings found in this section, all indicate that the buds are the chief means of multiplication.

One of the most noticeable features of the corms as collected in the field, is their lack of symmetry and their oblique position (PLATE 3, FIGS. 50, 51). It is quite rare to find mature corms more nearly symmetrical than the one in PLATE 5, FIG. 69. In many cases this is certainly due to displacement by the trampling by animals; but in the writer's opinion, it is more often due to the formation of an unequal number of roots on different sides of the bud. This unequal distribution causes an upsetting of the corm

late in the season when the roots shorten and produce the so-called root pull. This opinion has been strengthened by the fact that pot cultures in which the corms were carefully placed in an upright position, always show many of the corms tilted and some almost inverted after one growing season.

THE ROOT SYSTEM

The roots of *A. triphyllum* seedlings have been briefly described by Rennert (**22**, pp. 46, 47), as being of two forms, a group of two or three short, slender primary roots and a group of three secondary roots. The latter appear after the primary, have an origin higher on the corm, are larger and longer than the primary, and are contractile. Both primary and secondary roots are diarch in structure. To this the writer would add that in all seedlings examined he has found but one primary root, and it is diarch in structure. The later roots are either triarch or tetrarch.

In mature plants Rimbach (**24**) has reported two groups of roots in *A. Dracontium*, and then adds, "*Arisaema triphyllum* (L.) Torr. resembles perfectly *A. Dracontium* in the behavior of the underground organs" (**24**, p. 175). According to this author there appears at the beginning of the growing season a circle of long slender simple roots which extend in a more or less horizontal direction. Later a second group appears slightly above the earlier roots. These are robust, long, simple roots which grow nearly directly downward. They show a marked contraction shortly after their formation. All roots are deciduous, being separated from the corms about the time of ripening of the fruit. The present writer has found a varying thickness of 1–2.5 mm. in the roots of mature corms of *A. triphyllum*, and perhaps two groups in time of origin, although the demarcation between the two is not as

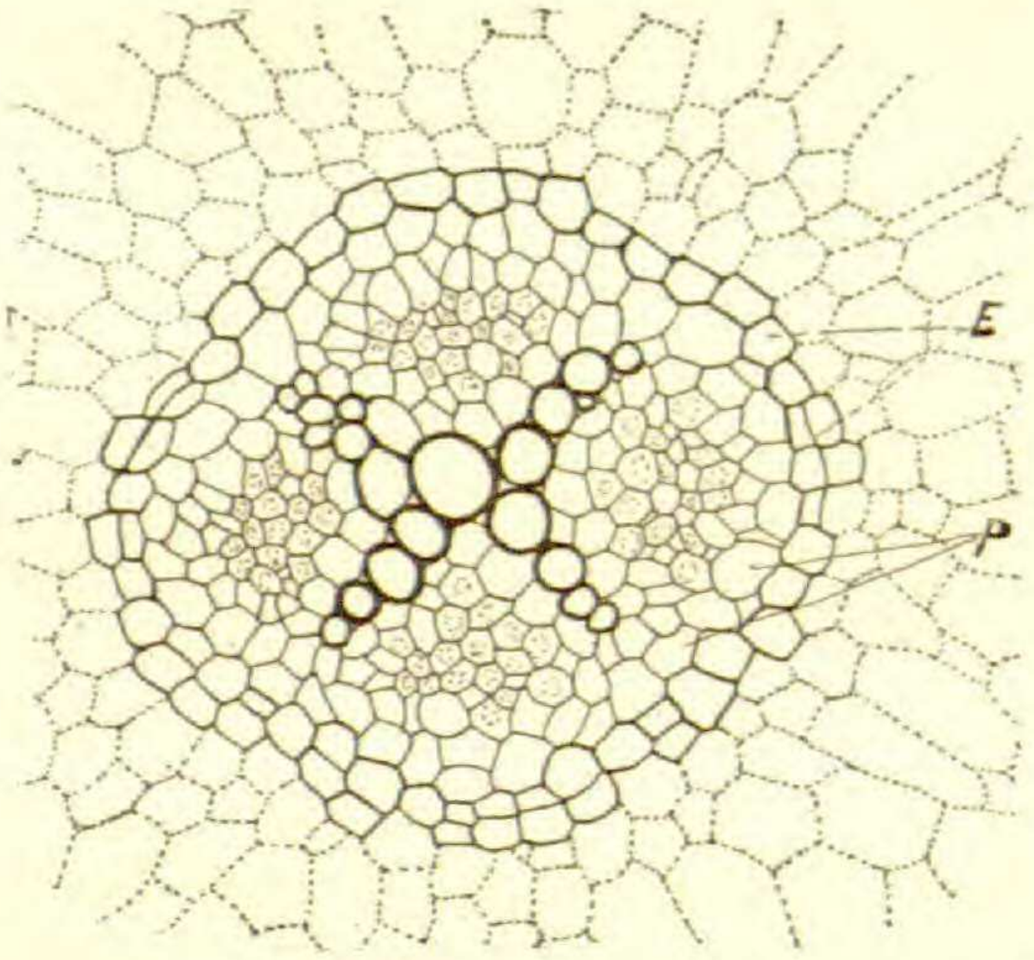


FIG. 35. Cross section of a tetrarch stele, showing clearly marked but irregular endodermis, *E*, and pericycle, *P*. × 160.

distinct as reported by Rimbach for *A. Dracontium*. The mature roots show many branches near their tips (PLATE 5, FIG. 69). In section these roots show a three- to five-radiate stele with a distinct endodermis of one to two rows of thickwalled cells (PLATE 5, FIG. 66; TEXT FIG. 35). Around this is a thick cortex of parenchymatous cells, small next to the endodermis but much larger and torn or distorted near the dark and more or less corky epidermis.

As to the contractile feature of the roots of mature corms, the statement of Rimbach (**24**, p. 172) that the contraction may amount to 40 per cent. in the basal portion and a total of 15 mm. or more for the whole root in *A. Dracontium* seems to hold equally well for *A. triphyllum*. The work of De Vries (**8**) and Rimbach (**23**) has left nothing to be added to this subject from a study of *Arisaema*. A point of interest appeared in the cutting of longitudinal sections of mature roots. The material had been killed in hot acetic alcohol and embedded in paraffin in the usual way. The transverse cortical ridges or wrinkles were quite prominent, but the stele seemed to be in normal position. As soon as the sections were cut, however, they became very much twisted and crumpled. Examination with the microscope showed the usual distortion of the outer cortical cells, an inner region of undisturbed cells, and then the stele section all twisted and folded (PLATE 5, FIG. 68), as though it had been held in position by the rigidity of the surrounding zone of cortical tissue.

The minute structure of a growing root tip of *A. triphyllum* shows a feature which seems unique. At the root tip (PLATE 5, FIG. 67) the usual angiosperm type is evident in the formation of a dermatogen, periblem, plerome, and root cap more sharply marked than in the onion. But at a point about the width of the root from the tip, there appear in the third and fourth layer of cells inside the dermatogen, large, elongating cells in every way similar to those forming the primary xylem elements in the plerome (PLATE 5, FIGS. 63, 64, 65, 67). These cells increase in length and finally unite to form continuous tubes in the outer cortex of the root. Their walls remain unchanged and the cavities are at a very early period filled with bundles of raphides.

LEAF STRUCTURE AND DEVELOPMENT

The seedling leaves of *A. triphyllum* are simple, cordate to ovate abruptly acute, with a slightly cordate base. The blades are from 5 mm. wide by 10 mm. long to 20 mm. wide by 30 mm. long. The venation is reticulate, pinnate, with two prominent basal branches "foreshadowing distinctly the plan of the mature trifoliolate leaf" (**22**, p. 48). The margin is very finely toothed. It is slightly membranaceous and crisped. The upper surface is glabrous, shining at first but becoming dull with age. The lower surface is distinctly glaucous after the leaf is fully expanded. The petiole may vary from 4–20 cm. in length. Its enlarged, hollow base covers almost entirely the new terminal bud of the corm. PLATE 4, FIG. 58, shows a small group of average seedlings.

The primordium of the first leaf is laid down some time before the seed is matured, and in the mature embryo the regions of petiole, midvein and lamina are clearly marked (TEXT FIGS. 21, 22). During germination the blade develops rapidly, and, closely rolled, is pulled from the soil by the lengthening of the petiole, which usually arches in its escape from the cotyledon. PLATE 3, FIGS. 34–39 show the normal seedling leaf blade from its first appearance to its final expansion. Occasional lobed leaves suggestive of the later compound leaves are found. Such a form with two lateral lobes symmetrically placed is shown in PLATE 3, FIG. 43.

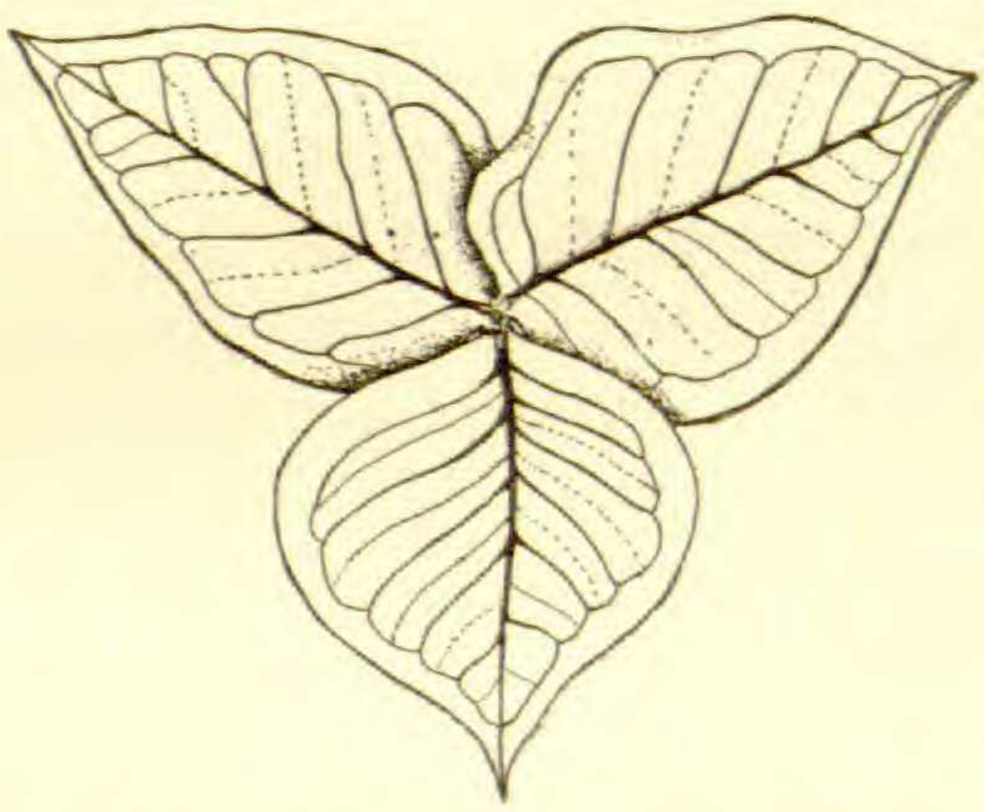


FIG. 36. A second year leaf, showing form and venation. × 1.

The leaf of the second year is typically trifoliolate (TEXT FIG. 36) and in all but size is like that of the mature plant. The leaflets are ovate to cordate, sessile, with acute apex and cordate to slightly tapering base. The lateral leaflets are slightly larger and less symmetrical than the terminal. They are pinnately net-veined with surface and margin as in both younger and older leaves. The leaves range in size from 3.5 cm. wide by 2 cm. long to 8

cm. wide by 5 cm. long, with petioles 4–12 cm. long. These leaves come through the ground with all leaflets closely rolled, the laterals appressed to the petiole, the terminal erect and the whole inclosed in a long sheathing kataphyll (PLATE 3, FIGS. 46, 52). PLATE 3, FIGS. 40–42, show the position of the leaflets of the second year leaf. As shown by the cross section diagram in PLATE 3, FIGS. 53, 54, the leaflets are incompletely convolute. In the placing of the leaflets and their escape from the bud the seedling in its second year shows all the characteristics of the mature plant. TEXT FIG. 1 and PLATE 3, FIGS. 44–46, 52, show the leaves of mature plants and such changes as follow the appearance of a second leaf or a flower cluster. After the appearance of the first trifoliate leaf the only change to be noticed in the next four or five years is increase in size. Leaves of mature plants may reach an extreme width of 35 cm., with middle leaflet 25 cm. long and with petioles up to 45 cm. in length.

As is well known, plants showing the same general maturity and even the same size and development of leaves differ in that some will produce but one leaf and others two. Seedlings produce but one leaf each season up to the time of the first inflorescence. After that time all gradations in development have been observed from plants without any suggestion of a second leaf, through those with rudimentary leaves inclosed in the petiole of the first leaf, to plants with two normal leaves almost equal in size. There seems to be no time limit for the appearance of the second leaves after the first inflorescence, and no uniformity in their size when first produced.

As has been stated, the leaves of *A. triphyllum* are net-veined. The system of each leaflet consists of a mid-vein with five to ten strong lateral veinlets with an equal number of weaker laterals between them, and all joining their extremities with a continuous vein extending around the leaf at a distance of 3–8 mm. from the margin (TEXT FIG. 36).

In minute structure, leaves from plants of different age show no noteworthy differences. As seen in section (TEXT FIG. 37) the leaf has a typical mesophyte structure. A single layer of epidermis, with the outer walls slightly cutinized, covers each surface. Next to the upper epidermis is a single layer of short

palisade cells. The remainder of the space is filled with a mass of rather loose, spongy parenchyma, in which the smaller veins are imbedded. The veins are composed of a few spiral ducts and tracheids (TEXT FIG. 37, *B*) near the upper epidermis, from which they are separated by three or four layers of long, thin-walled non chlorophyll-bearing cells (TEXT FIG. 37, *A*) and a small irregular group of phloem elements below (TEXT FIG. 37, *C*). The stiffening factor is a prominent strand of collenchyma (TEXT FIG. 37, *D*) making up the greater part of the ridge on the under side of the leaf.

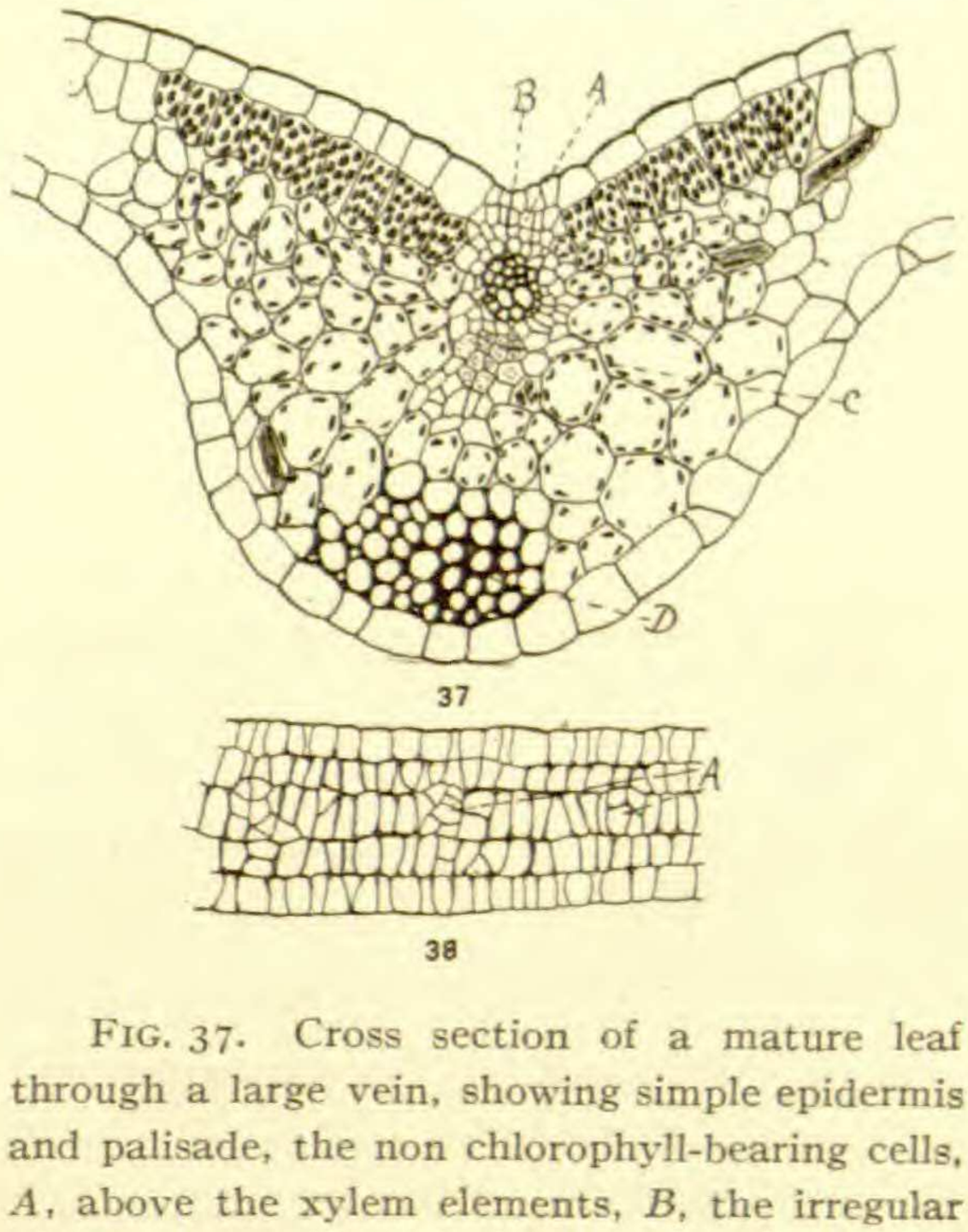


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FIG. 37. Cross section of a mature leaf through a large vein, showing simple epidermis and palisade, the non chlorophyll-bearing cells, *A*, above the xylem elements, *B*, the irregular phloem area, *C*, and the strong collenchyma strand, *D*. × 52.

FIG. 38. A cross section of a young leaf with the first signs of differentiation of cells indicating the position of vascular strands, *A*. × 52.

In surface view the lower epidermis shows irregular cells more or less interlocked by means of undulating walls (TEXT FIG. 39). The stomata average 50 to the sq. mm. and show an average extreme width of 28 microns and an average extreme length of 40 microns. Adjoining the guard cells is a pair of accessory cells (TEXT FIG. 39, *A*). These accessory cells are sisters of their contiguous guard cells and are formed by a second division of the initial cell. Occasional twin stomata (TEXT FIG. 41) have been observed, which have probably resulted from a division of the cells which usually form guard cells. The upper epidermis is composed of cells with much more regular outline, and usually shows no stomata (TEXT FIG. 40).

As the blade appears in the differentiation of the primordium it is composed of five layers of similar cells (TEXT FIG. 38). The

differentiation of certain cells (TEXT FIG. 38, *A*) of the middle layer to form the primary vascular elements occurs first. The epidermis is clearly marked next, followed by the formation of the palisade cells by the top of the three inner layers and the formation of the spongy parenchyma by the lowest layer and the remainder of the middle layer. There is practically no variation in leaf structure coincident with changes in conditions of growth. The petioles of plants grown in the shade are slightly longer than of those grown in full light, and the size of the blades may vary from year to year; but the change in thickness due to increased palisade formation found in leaves of many plants following change from weak to strong light, is not at all evident. A slight increase in the number of stomata, and the occasional appearance of a few stomata on the top of leaves of shade plants has been noted. So far, however, experiments have failed to show whether these changes are the result of different conditions or merely indicate individual variation.

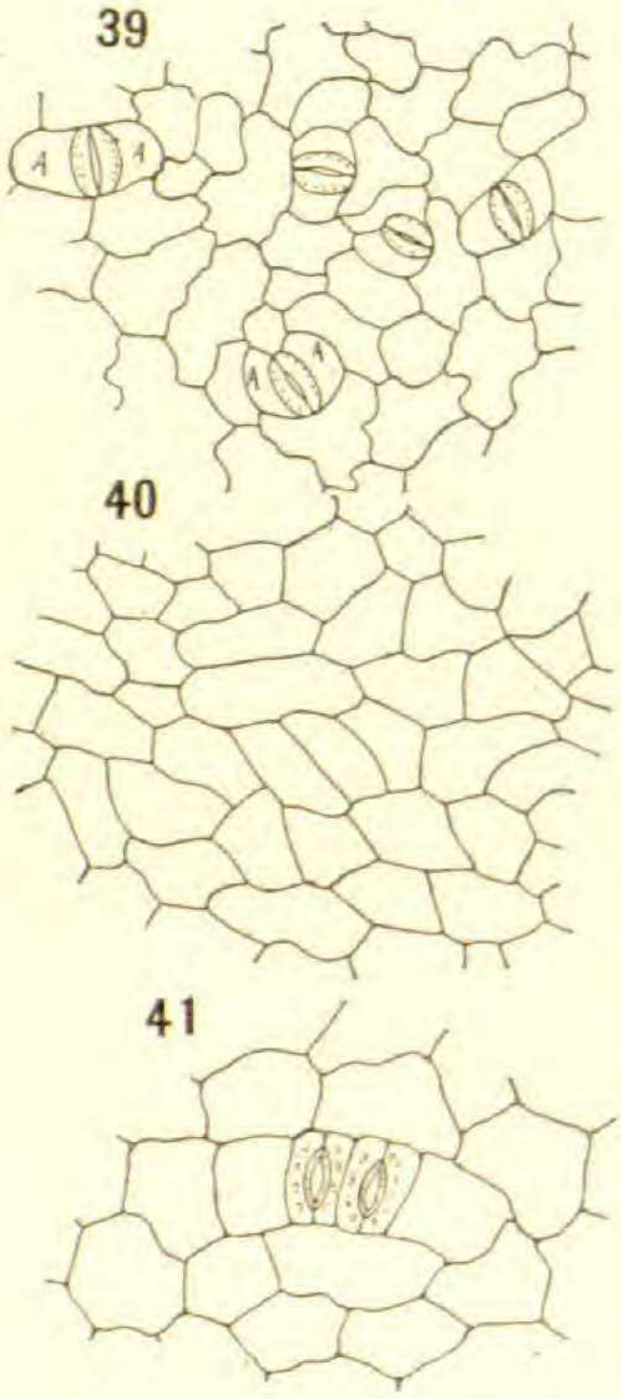


Fig. 39. Surface view of lower epidermis. *AA*, accessory cells.

FIG. 40. Surface view of upper epidermis.

FIG. 41. Twin stomata from lower epidermis.

STRUCTURE OF PETIOLE AND SCAPE

The vascular system of embryo, root and leaf are treated in these sections. The similarity of structure of petiole and scape make possible a common description. These bodies are composed of a peripheral layer of epidermis with slightly thickened walls, and two or three underlying layers of small parenchymatous cells. Inside this peripheral portion is a circle of well developed vascular bundles, each with a strong strand of collenchyma separated by one layer of cells from the epidermis (TEXT FIGS. 43, 44). The vascular elements of these bundles consist of a few spiral ducts and phloem elements, and are duplicates of the principal veins of the leaves. The inner portion of both petiole and scape is

composed of air spaces divided by chains and plates of parenchymatous cells, with vascular bundles scattered promiscuously through the spongy mass (TEXT FIGS. 42–47). The vascular

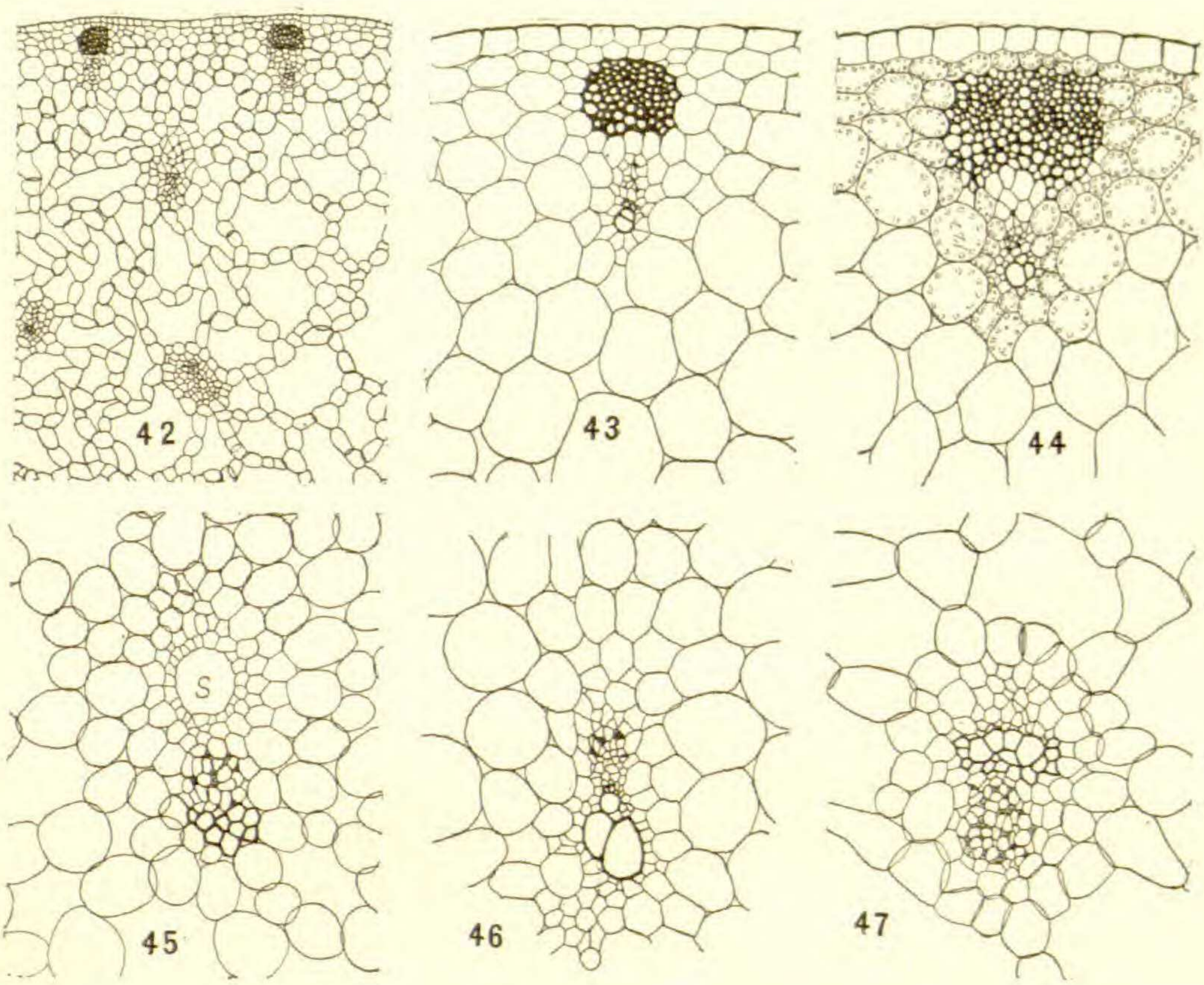


FIG. 42. Part of a cross section of a scape, showing peripheral region with bundles having strands of collenchyma, and the large air spaces of the pith. × 20.

FIG. 43. An average peripheral bundle from a petiole. × 65.

FIG. 44. An average peripheral bundle from a scape, showing chlorophyll-bearing cells. × 65.

FIG. 45. A bundle from the pith of a petiole. *S*, schizogynous vessel. × 65.

FIG. 46. Average bundle from petiole pith. × 65.

FIG. 47. A large bundle from scape pith, showing large phloem area. × 65.

bundles of the pith region are, as a rule, similar to those of the periphery, but lack the strand of collenchyma. There is considerable difference in the size of the bundles, some showing only one or two small ducts and a corresponding number of phloem elements, while others show as high as twenty xylem elements. In general, the bundles of the scape are larger than those of the petiole and greater proportionate phloem area, as will be evident from a comparison of TEXT FIGS. 45 and 46 with TEXT FIG. 47.

There is not in any case a distinct bundle sheath, the vascular elements being surrounded by chlorophyll-bearing parenchyma. The presence of chlorophyll in the cells bordering the vascular elements is so marked as to give a striking appearance to cross sections, which show all but the innermost bundles distinctly green.

THE RAPHIDE CELLS

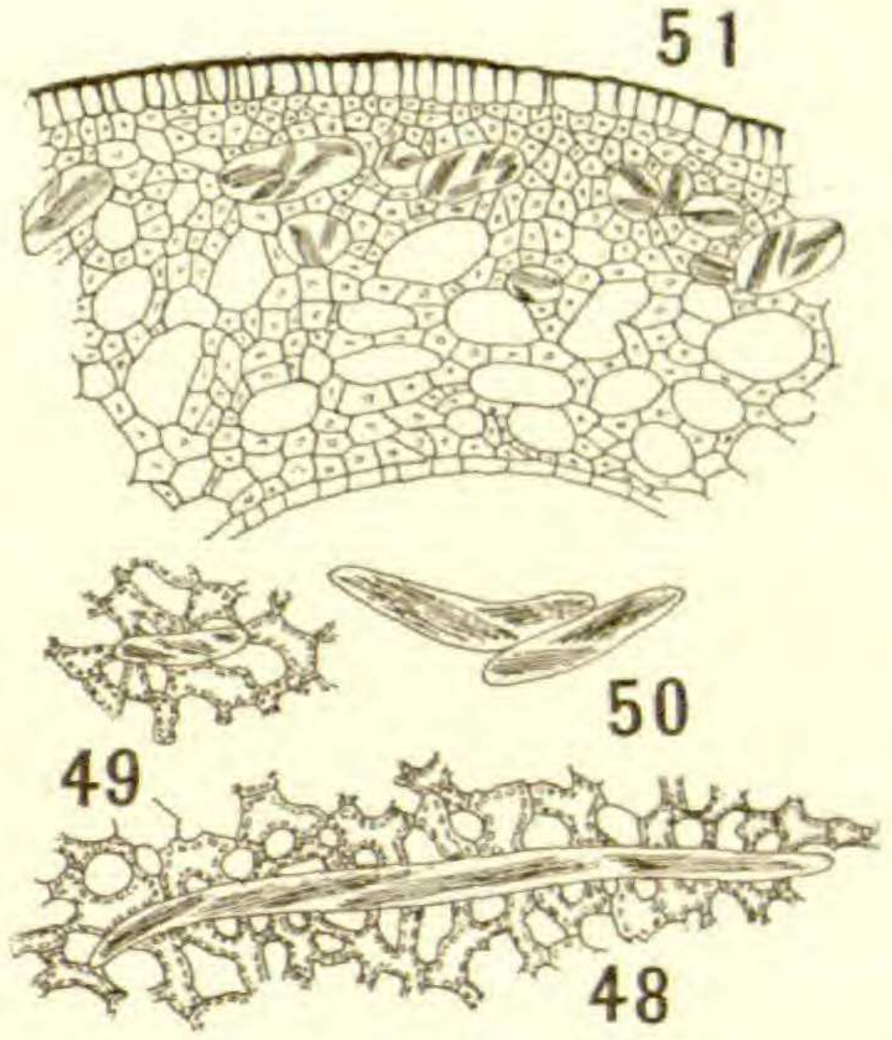
From the first, *A. triphyllum* has been noted for its intensely acrid sap. This feature alone is sufficient to protect its green parts and the corm with its store of starch from the ravages of animals of all sizes. The North American Indians are reported by Havard (**16**, p. 106) to have found that by drying and cooking, the corms could be made edible. Sometimes in laboratories it is considered a lark to cook and eat Indian turnip corms. The writer has found them quite palatable when cut up and boiled for a half hour or more with one or two changes of water.

The irritating principle is the raphides of calcium oxalate which are found abundantly through the plant, and which are always floating free in the sap exuding from wounds. Barnes (3) found that by filtering the expressed sap twice through filter paper, and so removing the needle-like crystals, it lost all its acridity. Attempts by the writer to find any volatile oil or other irritating substance have given but negative results.

The raphide-bearing cells are found almost throughout the plant. They have not been found in the mature embryo, in root caps, within limits of vascular strands or in epidermal structures. They are especially plentiful in leaf laminae, fruit, and corm.

In the leaf the specialized cells occur in palisade or spongy tissue and are often close beside veinlets. Here they are for the most part long, more or less sinuous cells with fascicles of crystals extending in the general direction of the long axis of each cell (TEXT FIGS. 48–50). The size and shape of the cells may vary in one part of the plant, as shown in the figures just cited. Even wider variation is to be found in different parts of the plant. In the scape, spadix and petiole the cells are found chiefly near the periphery and are similar to those in the leaf. In the corm some cells ares lightly larger and more globular than those containing starch, and they contain numerous small bundles of raphides

lying in different positions (TEXT FIG. 28 *a*). These cells are much more abundant in the outer portion of the corm. In the endosperm the few raphide-bearing cells are similar to those in the corm but are smaller. In the walls of the ovary and maturing fruit the cells are chiefly in the upper portion, where they form a distinct area (PLATE 2, FIG. 26; TEXT FIG. 51). Probably the most clearly defined raphide region is that in the root. Here, as described in the section on root structure, certain cells in the outer periblem are differentiated shortly above the growing tip and form almost continuous receptacles for long lines of raphide bundles (PLATE 5, FIG. 65). Wherever found the raphide cells are differentiated very early. They rapidly increase in size, retaining their protoplasmic lining and a living nucleus long after the central vacuole has been filled with bundles of crystals.



FIGS. 48–50. Different forms of raphide-bearing cells in the leaf mesophyll. × 52.

FIG. 51. Raphide-bearing cells in the outer portion of the ovary wall. × 52.

SEX DISTRIBUTION

Although *A. triphyllum* is usually considered a dioecious plant, spikes bearing both staminate and pistillate flowers are frequently found. From the examination of hundreds of plants through three consecutive years the writer finds the ratio between staminate and pistillate spikes about 3:2, and 8–10 per cent. of the whole number mixed. The type of a mixture most often found is that of a spike bearing chiefly pistillate flowers and a few staminate flowers at the upper or lower end or at both upper and lower ends (PLATE 1, FIG. 23; PLATE 4, FIG. 55). Usually the number of staminate flowers is less than shown in FIG. 55. Occasionally the ratio is reversed, and a spike shows a few pistillate flowers scattered through a mass of staminate flowers as in PLATE 4, FIG. 60. PLATE 4, FIG. 57, shows

an extreme case with one well developed ovary, apparently with fertilized ovules, borne on a staminate spike near its base. It has been observed that when any considerable number of pistillate flowers are present, the thickened axis characteristic of the pistillate spike is evident. Usually all the flowers borne on mixed spikes are normal in form and functional development. Peculiarities in form and position of staminate flowers are frequent enough for mention. The growth of such flowers on an extension of the spike axis as in PLATE 1, FIG. 22, is not uncommon. A variable number of flowers may appear so, sometimes but two or three, and again enough to give the appearance of a staminate spike above the pistillate as in *A. Dracontium* and other aroids. In a few cases the staminate flowers are borne on long pedicels (PLATE 4, FIG. 59) and show peculiarities of structure. Those forms, along with others showing a tendency to bisexuality, are more fully discussed in the section dealing with teratology.

It has been noted elsewhere that the number of leaves seems to depend upon age and the abundance of food, the older, well-nourished plants producing two leaves, the younger plants but one. There seems to be no relation, however, between the leaf development and the sexuality of the plant, the ratio of pistillate and staminate spikes being about the same with plants bearing one leaf as with those bearing two.

It has been generally recognized by students that the sex of plants of *A. triphyllum* may change. The first published attempt to determine anything experimentally concerning this point was by Atkinson (1). A report of this work was given at the Ithaca meeting of the Society for Plant Morphology and Physiology (December 28–29, 1897). The published abstract is quoted here in full:

"Female, male, and neuter plants, the history of which was known by growing them in pots for one season, were potted, some in rich soil and others in poor soil, the object being to change them from male to female, etc., by varying amounts of nutriment. Male plants in rich soil were in one year changed to female, and large neuter plants in rich soil were changed to female.

"In a second series, two large two-leaved female plants, with large bulbs, were selected at the time the fundament of the flowers

was formed. The bulbs were cut so as to remove all but a small portion in connection with the bud. By this removal of the larger part of the stored food the plants were changed to male."

Gow in 1913 (14) made the statement that these plants probably alternate in sex from year to year. In proof of that theory he stated that plants which had borne pistillate flowers one year produced staminate flowers the next season after being transplanted.

The present writer has made rather extensive attempts to duplicate the experiments of Atkinson, but has encountered two serious difficulties, viz., many of the corms have been partly or wholly destroyed by fungi, and there seems to be no way to determine certainly when the flower initials are being formed. The wide variation in the time of flower development is discussed in another section, and it need only be said here that two plants of a group rarely show the same stage of development, the range in staminate spikes being from bud initials to completed tetrads in late July. This would mean a possible difference of six weeks in the formation of the flower fundaments of plants in one group. From this it is clear that any experiment depending upon uniformity of development would be open to question. The history of the experiments as performed and the results follow. Robust plants which bore purely pistillate spikes were dug up the first week of June, and after having the lower two thirds of the corm cut away and being allowed to form a dry callous by two days' exposure to the sun and air, were planted in rich loam. Through the year these cultures were treated just the same as others that were in every way normal. The following spring a part of these corms produced flowers, and all the flowers were staminate. Their growth was not normal, however, and all the plants were small and variously deformed. Some produced leaves only, and three of the plants produced inflorescences only without leaves. This goes to show merely that the primary effect of the mutilation was a serious disturbance of the general system of nourishment. The same spring some three hundred corms were reset for experimental purposes, the collecting being done in late May and early June. Those plants which had borne only pistillate spikes were carefully kept apart. All were planted in rich, moist loam and watered

occasionally through the year. Of this bunch of plants reset early in the season—before the flowers were formed—but three produced pistillate spikes the next year.

Yet another observation must be noted here. The spring of 1913 was peculiar in southern Indiana because of a flood condition in March and April (a rainfall of 14.34 inches was recorded between March 23 and April 30) followed by extreme drought. The result upon *A. triphyllum* was that by June 1 all plants except those near springs or at the margins of water-courses, were withered and dead. As has been stated above, the usual ratio of staminate to pistillate spikes is about 3:2. A careful count of plants in the spring of 1914 showed among those not near a water supply a ratio of about 70 staminate to 1 pistillate, while among plants near springs, in perennial marshland, and in shaded, damp ravines, the usual ratio held. The change in ratio in passing from the damp bottom of a deep ravine to the top of the side was quite noticeable. Along the waterway the usual number of pistillate flowers were in evidence, while on the upper part of the slope where growth had been checked by the early drought of the previous summer, only staminate spikes could be found. Such a difference is not usual; and it seems that its appearance in 1914 is in some way related to the short growing season of 1913.

It has been observed that the usual ratio between staminate and pistillate spikes holds from year to year in limited areas with a non-failing or late failing water supply. This is true without regard to soil, as shown by colonies growing in leaf mold between limestone fragments, others in deep, rich loam of moist woodlands, and yet others in the poor, recent clay of young ravines. Plants do not grow with equal vigor in the different kinds of soil, but the difference in available food seems to influence the vegetative development primarily, and the sexual development little, if at all. One particular colony of about fifty plants growing on a steep clay bank, slightly shaded, but well watered by seepage from underlying limestone has been observed closely. The plants average 1.5 dm. in height, the largest specimen being 2 dm. high. The petioles are slender and the corms undersized, but the flower spikes show the usual ratio of males and females.

One point from experimental work should be noted here.

Sturdy plants bearing pistillate spikes have been transplanted to beds of gravel and of *Sphagnum*, receiving only such food as was carried by the tap water with which they were abundantly supplied during the growing season. These plants continue to produce pistillate spikes after two years of such treatment. In the meantime the corms of these plants show a marked decrease in size as a result of their failure to store up as much food as is required for the year's growth.

The writer cannot agree with Gow's statement that there is an alternation of sex characters. Several old vigorous plants under observation in favorable situations for five years have not failed to produce pistillate spikes each year. To this it may be added that in cultures of plants grown from seed, the first flowers produced have been staminate. The time of the first change from staminate to pistillate is not fixed although it usually occurs in vigorous plants two or three years after the first flower spike is produced. Subsequent changes in sex may be accomplished without noticeable checking of the vegetative increase of the plant. For example, the early transplanting of corms, while changing the sex for the next year, need not reduce the size or number of leaves produced.

From the observations given above, the following conclusions seem warranted. There is not an alternating or cyclic change in sex in *A. triphyllum*. The amount of food stored in the corm does not determine the sexual condition. The amount of solid food does not determine the sexual condition, but a shortage of water and consequent checking of growth at the time of the beginning of flower formation produces staminate flowers. The checking of growth at that critical time is the important factor introduced by the early transplanting, by the removal of the corms for mutilation by Atkinson and the writer, and by the early drought of 1913, The influences effecting change of sex are not the same as those producing changes in the vigor of vegetative growth.

TERATOLOGY AND VARIATION

Rennert (21) in 1901 gave a brief account of the teratological phenomena recorded for *A. triphyllum*. The notes referred principally to the dedoublement in the case of flowers and leaves

and to monstrous development of spathe or spadix. The most interesting reference, perhaps, is that to a report by Foerste (12) in which there is described a confluence of two leaf petioles and two leaflets and a partial confluence of two inflorescences. Phenomena closely related to this are not rare, and doubtless result from a duplication of initials in the early bud formation. The confluence of parts has been observed in all degrees, and in young and old, sterile and flowering plants. The petioles may be

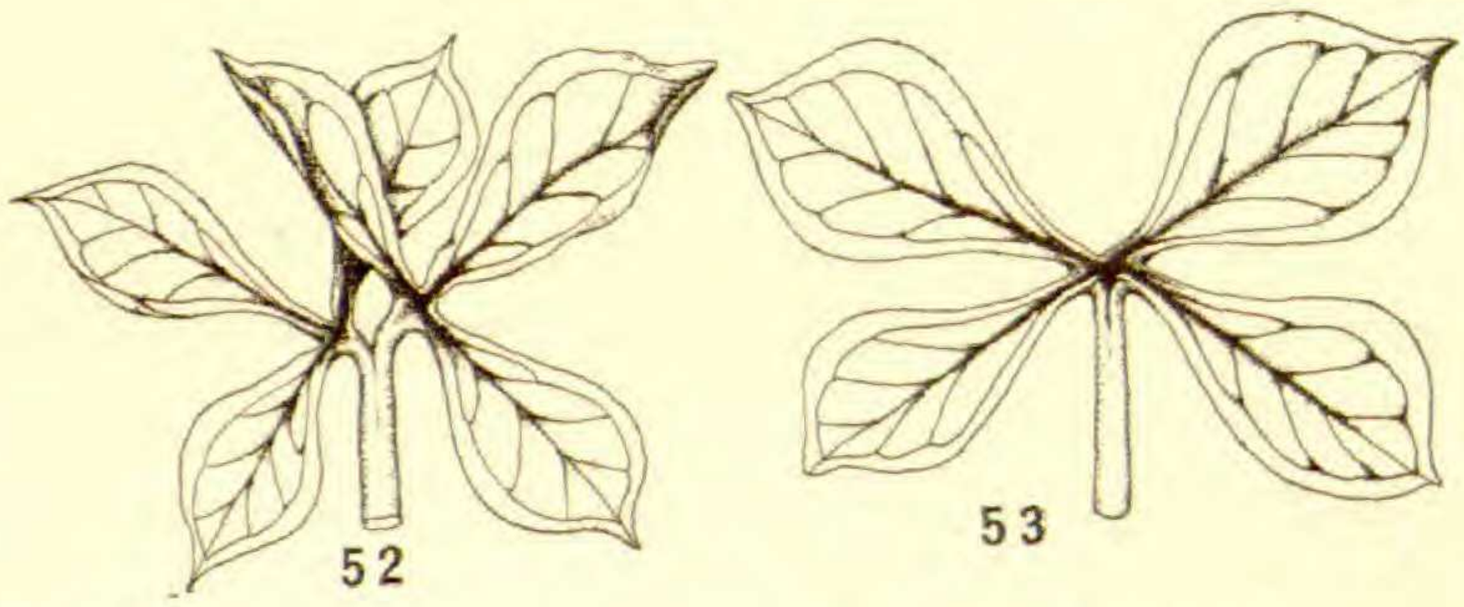


FIG. 52. Two leaves with almost entirely confluent petioles. × one sixth.

FIG. 53. A leaf with four leaflets, one of a group, all of which showed this character. × one sixth.

attached together but a short distance from the corm or the connection may extend almost to the laminae (TEXT FIG. 52). The same is true of inflorescence, the attachment being in any degree from the doubled peduncle and separate spathes to the single spike with two sterile spadix sections as figured by Rennert (21, *f.* 2, *M*), or with a branched spadix as in PLATE I, FIG. 19.

These peculiar formations are in no way related to the formation of two leaves by the old, vigorous plants, for, in that case, there is no confluence, one leaf initial being inside and of later formation than the other. In normal two-leaved plants the petiole of one leaf is enveloped by the other and the scape surrounded by both (TEXT FIG. 70).

As in seedlings an occasional lobed leaf appears, so in older plants, there is sometimes found a leaf with the leaflets more or less united, usually so that the leaflets appear as lobes of a deeply divided leaf. Such forms are most often seen in two- and three-year-old plants.

Rennert (21) also describes and figures a few clusters in which the spathe has failed to develop, appearing only as a scale below

the flower spike, and another in which the sterile portion of the spadix formed an irregular monstrous form. Plants have been observed by the writer in which the spathes were contorted and reduced in size as the result of evident injury; and the fact that the spathe begins its development before the differentiation of the spadix would make possible an injury which would entirely check the spathe's development at a time when no harm would come to the spadix. As noted in connection with the experiments on change in sex, some plants with mutilated corms produced inflorescence only. One such flower cluster showed a normal spathe with normal staminate spike of flowers, but with a mere knob to represent the sterile spadix. Later two similar specimens were collected in the field.

The only definite report of observations of abnormalities in the form of individual flowers is that of the confluence of the stigmas of two separate ovaries, reported by Rennert (**21**, p. 248). The occurrence of mixed spikes has been discussed in the section on sex distribution. It was there stated that the staminate flowers found on spikes chiefly pistillate were usually normal and functionally perfect. In some cases, however, the stamens are borne on long pedicels (PLATE 4, FIG. 59) and show either small, sterile anthers or bract-like sterile growths. Many of the stamens formed entirely above a pistillate spike are undersized (PLATE 1, FIG. 22), and some do not mature pollen. Close observation of a large number of flower spikes shows that there are three lines along which the flowers may vary from the normal form. The most common is that just mentioned and represented in PLATE 4, FIG. 59, i. e., the more or less complete transformation of floral into vegetative structures. This is found not only with staminate flowers but is very frequent on otherwise purely pistillate spikes, where the transformed parts appear as more or less convolute bracts (TEXT FIGS. 54, 55). A second line of abnormal development is that represented by the confluence of parts. The confluence of the short filaments of stamens and of anthers was mentioned in the section dealing with the staminate flower. The confluence of stigmas as reported by Rennert has been noted. An extreme case of the last named peculiarity is shown in TEXT FIG. 56, where four distinct ovaries have a common stigmatic brush. Close examination

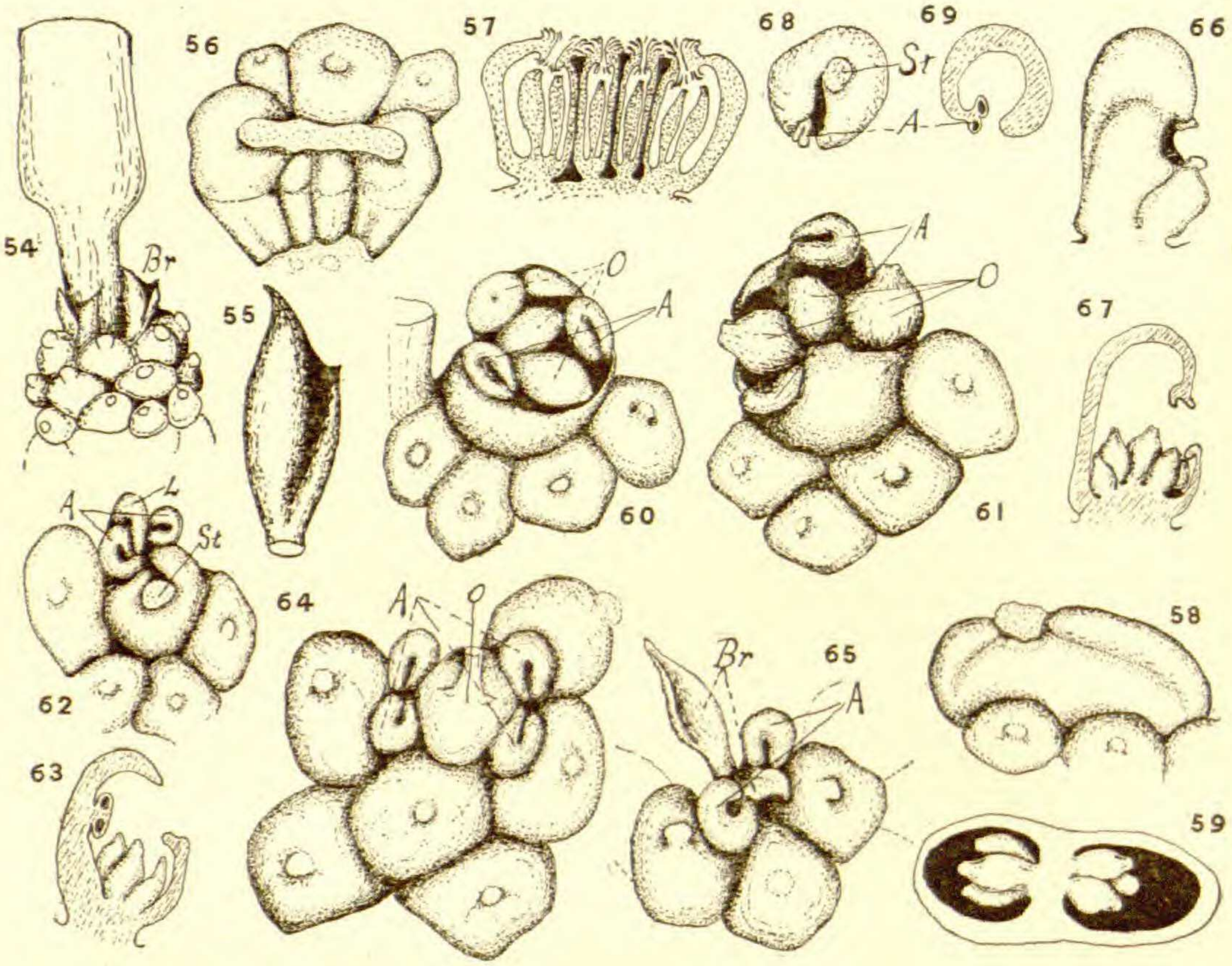


FIG. 54. Top of a pistillate spike, showing sterile bracts, *Br*. × 1.

FIG. 55. One of the bracts shown in 54, enlarged. × 3.

FIG. 56. A group of ovaries with apparently confluent stigmas. × 3.

FIG. 57. A diagrammatic section of group in FIG. 56, showing the ovaries and stigmas really distinct. × 3.

FIG. 58. A double ovary. × 3.

FIG. 59. A cross section of the ovary shown in FIG. 58, showing the ovules attached to the median wall. × 3.

FIGS. 60, 61. Two views of a flower with three functional ovules, *O*, and two functional anthers, *A*, on a partly suppressed ovary wall. × 3.

FIG. 62. A cleft ovary with normal stigmas, *St*; a bract-like lobe, *L*; and two anthers, *A*. × 3.

FIG. 63. A section of the ovary shown in FIG. 62, showing well-developed ovules. × 3.

FIG. 64. A flower with one ovule, *O*, the ovary walls almost entirely suppressed and bearing four anther cells, *A*. × 3.

FIG. 65. A structure without ovary walls, bearing two anthers, *A*, and instead of ovules, two sterile bracts, *Br*. × 3.

FIG. 66. An abnormally developed ovary with functional ovules in the base, but with the style, *S*, unclosed and its surface without stigmatic hairs. × 3.

FIG. 67. A section of the ovary in FIG. 66. × 3.

FIG. 68. A cleft ovary with normal stigma, *St*, and a two-celled anther, *A*, on the wall margin. × 3.

FIG. 69. A cross section of the structures shown in FIG. 68. × 3.

shows structures of this type to be only superficially confluent. TEXT FIG. 57 shows a vertical section of the ovaries shown in TEXT FIG. 56. It seems that the crowding of the young ovaries prevents the usual closing of the stylar opening, and the subsequent development of hairs on the increased stigmatic margin, forms a seemingly continuous brush. A better example of true dedoublement is shown by the two-celled ovary figured in TEXT FIGS. 58, 59.

A third line of divergence leads towards bisexual flowers. As might be expected, many such flowers are found on spikes bearing both staminate and pistillate flowers. The specimens here described, with many other similar forms, were collected in the field, where they had grown under usual conditions. TEXT FIGS. 60, 61 show two views of a flower with a partially developed ovary wall, three normal ovules, and two functional anther cells. TEXT FIGS. 62, 63 show an ovary with normal stigma and ovules, and with two functional anther cells on a lobe of the ovary wall. TEXT FIG. 64 shows a flower with the ovary wall almost entirely suppressed, four functional anther cells and an unusually large ovule. TEXT FIG. 65 shows a flower with two functional anther cells, and instead of ovules, two sterile bracts similar to those in TEXT FIGS. 54, 55. TEXT FIGS. 66, 67 show a flower with an unusual ovary wall suggestive of that in TEXT FIG. 62, and with functional ovules, but without any anther. In TEXT FIGS. 68, 69 is shown a cleft ovary wall with normal stigma and two sterile anther cells, but with ovules entirely suppressed. It should be noted that in all bisexual flowers examined the anther formation has been connected with the ovary wall. In no case has there been found a suggested transition from ovule to anther, even when the ovule shows degeneracy, as in TEXT FIG. 65, or suppression as in TEXT FIGS. 68, 69.

Quite distinct from the abnormalities just described are the following. A group of ten plants, probably arising from one corm and its offshoots, was found with leaves having four leaflets as shown in TEXT FIG. 53. The plants were of medium size with normal inflorescence and leaves normal as to size, surface, and texture. All the plants showed a severe attack of *Uromyces Caladii* and died before another growing season made possible farther

examination and breeding experiments. On a damp, thickly wooded hillside near Trevlac, Brown County, Indiana, in the last four years about a dozen specimens have been found, each bearing two leaves and two flower clusters (PLATE 3, FIG. 47). There is no unusual character other than the production of the two flower clusters. These are of the same sex on each plant and are entirely independent, arising from two separate initial groups (TEXT FIGS. 71, 72). A few plants of a third form, having leaflets with a shining glabrous lower surface and petiolules 2–3 cm. long, have been found in the neighborhood of Bloomington, Indiana. Whether or not these are simply variant forms, true mutants or distinct varieties cannot be said until a more careful study and possibly breeding experiments can be made.

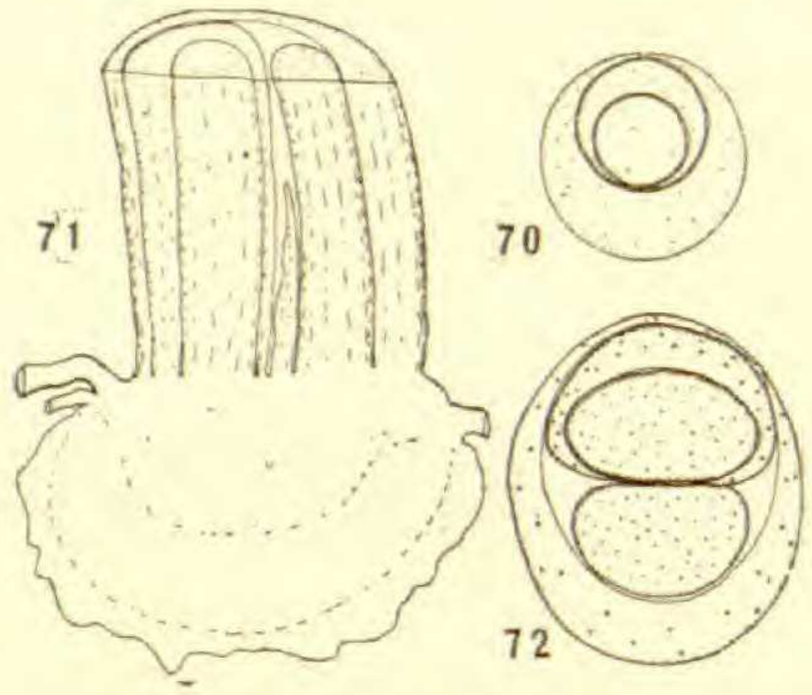


FIG. 71 is diagrammatic section of corm and bases of leaves and scapes of two-flowered plant, to show the distinct origin of the scapes. × ¾.

FIG. 72. Semidiagrammatic cross section of petioles and scapes of plant figured in PLATE 3, FIG. 47, and TEXT FIG. 71.

FIG. 70. Semidiagrammatic cross section of normal two-leaved plant to show position of petioles and scape.

THE RELATION TO UROMYCES CALADII

The only fungus parasitic upon *A. triphyllum* as reported by Saccardo is *Uromyces Caladii* Farl. Without going into a detailed account of the fungus, some observations of its influence upon the host under consideration may be given. The aecidia occur on the lower leaf surface, rarely on the upper, on petioles and scape, on both surfaces of the spathe and occasionally on the ovary walls and sterile spadix. The cups appear with or soon after the appearance of the leaves and flowers in spring. When the infection is severe, the parts attacked are deformed, the leaves being small and more or less rolled up, the spathe thickened and its hood shortened and erect, and the spadix is sometimes two to three times its normal size. The spermogonia have been found on the leaves and in the ovaries. Usually the spermatia are discharged

into the ovary cavity and float about in the slime there. Ovaries have been sectioned showing the micropyles filled with these bodies. Occasionally in this region teleutospores are formed in small scattered groups on the leaf surface.

Generally the floral parts suffer first and most from this fungus, although some plants are found with the growth evident only on the leaves. The affected plants are earlier in seasonal development than uninjured plants, as reported by Rennert (**21**, p. 250). Infected pistillate flowers develop early and the ovaries enlarge as after fertilization, but, as far as the writer's observations go, do not produce seed. It is a question whether or not normal embryo-sacs are developed. Plants once infected may live two or three seasons, but finally succumb to the ravages of the parasite. The appearance of rust on plants in culture the year following an early transplanting and removal of all stalks and leaves from the corm suggested the presence of perennial mycelium in the corm. Later examination of corms of infected plants has shown abundant mycelial threads in both the body of the corm and the terminal bud. Halsted (**15**) in 1894 made a brief report of observations on the distribution of the aecidia and teleutospores of *U. Caladii* on *A. triphyllum* but did not suggest the perennial nature of the mycelium.

SUMMARY

The additions and corrections presented in the present work may be briefly summarized as follows:

There is a very wide range in the time of development of the flowers, and a marked tendency toward the earlier development of staminate flowers.

The tapetal nuclei wander among the developing pollen spores in the anther cavity.

The ovule and the embryo-sac are of the lily type.

The ovary cavity is filled at maturity with slime produced by special hairs of the inner stigmatic brush.

A well-developed and complex permanent suspensor system is evident.

One daughter of the primary endosperm nucleus (fusion nucleus) undergoes two to four divisions while migrating to the micropylar end of the embryo-sac, and the resulting free nuclei

without taking a peripheral position initiate the endosperm formation by producing cross walls in various planes. Later endosperm growth is brought about primarily through the activity of a definite meristematic region.

The second daughter of the primary endosperm nucleus does not divide but organizes the residual cavity of the embryo-sac into a large nutritive cell which elaborates food material for the growing endosperm.

Pollination is secured by insect visitation. An unknown attraction for insects is evident in the pistillate inflorescence.

Primary roots of seedlings are diarch in structure. Secondary roots of seedlings and all roots of mature plants show a three- to five-radiate structure.

A small percentage of seedlings regularly do not produce functional plumules the first season.

The sex of mature plants is changeable, and the amount of water available at a certain period in development is directly or indirectly responsible for such change.

Abnormal flowers showing a tendency toward bisexual structure have been found.

The corms may harbor perennial mycelium of *Uromyces caladii*.

The writer wishes to express his deep appreciation of the kind interest and helpful suggestions of Professor D. M. Mottier of Indiana University, under whose direction the present work has been done.

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EXPLANATION OF PLATES 1–5

PLATE 1

FIG. 1. A nucellus with two completed tetrads of megaspores, five of which are germinating. × 210.

FIG. 2. Two tetrads of megaspores showing the lowest spore of each tetrad growing at the expense of the others. × 210.

FIG. 3. An embryo-sac with but little difference between synergids and egg cell, and the antipodals partly shrunken. × 210.

FIG. 4. A mature embryo-sac with an egg cell extending far below the synergids. × 210.

FIG. 5. A normal egg apparatus. × 600.

FIG. 6. An embryo-sac shortly after fertilization, showing one synergid, *Sy*, intact, the residual nucleus, *R*, and migrating nuclei, *E*, which have resulted from free divisions of one daughter of the primary endosperm nucleus. × 105.

FIG. 7. Whole upper portion of an embryo-sac shortly after fertilization, showing the nucellar cap, *N.C.*, two persistent synergids, *Sy*, the first division of the egg nucleus, *E*, the first mass of endosperm cells and the beginning of a plate formation at *P* by the division of cells. × 210.

FIG. 8. A proembryo with a divided suspensor, *Su*, and a four-celled embryo· (One cell entirely cut away.) × 210.

FIG. 9. A fertilized egg, *E*, and two synergids, *Sy*, imbedded in one large endosperm cell. × 210.

FIG. 10. A proembryo with one large suspensor cell, *Su*, and three embryo-cells resulting from nearly transverse divisions. × 210.

FIG. 11. Upper end of an embryo-sac showing remnants of nucellar cap, *N.C.*, path of the pollen tube, *PT*, and proembryo consisting of one suspensor cell, *Su*, and one embryo cell. *E*, *E*, *E* are the uppermost cells of the young endosperm. × 210.

FIG. 12. A proembryo with the suspensor cell, *Su*, divided before the first division of the embryo cell has occurred. × 210.

FIG. 13. A proembryo showing a divided suspensor and two embryo cells resulting from a vertical division. *Sy*, persistent synergid. *PT*, path of pollen tube. × 210.

FIG. 14. A proembryo with single suspensor cell, *Su*, two embryo cells resulting from a vertical division, the whole surrounded by the two large endosperm cells. × 210.

FIGS. 15, 16. Single berries from spike in Fig. 21. × 1.

FIG. 17. Longitudinal section of a berry, showing seeds in position. × 1.

FIG. 18. Cross section of a berry with five seeds. × 1.

FIG. 19. Upper portion of a pistillate spike and branched sterile spadix. × 1.

FIG. 20. A longitudinal section of a fruit cluster. × 1.

FIG. 21. A mature spike or fruit cluster with a few berries removed. × 1.

FIG. 22. A pistillate spike with a few isolated staminate flowers, male, above. × 1.

FIG. 23. A spike chiefly pistillate, with staminate flowers at both top and bottom. × 1.

PLATE 2

FIG. 24. Section of inner stigmatic brush and adjoining parts of the ovary, showing wax-filled hairs, *w*, *w*. × 42.

FIG. 25. Meristematic region, *M*, just above the lower border of the endosperm. × 42.

FIG. 26. Longitudinal section of style showing reduced papilla-like hairs, *P*, within. *R*, raphide cells. × 42.

FIG. 27. Longitudinal section of an ovule having a sterile nucellus, showing the changes in the integuments at the time of maturity of embryo-sacs in neighboring ovules. × 52.

FIG. 28. Bottom of an embryo-sac just after maturity, showing decomposition of nucellar tissue, *N*, and great elongation of contiguous cells, *I*, of the inner integument. × 52.

FIG. 29. A cross section of an almost mature anther. × 42.

FIG. 30. Longitudinal section of upper portion of embryo-sac shortly after fertilization, showing the mass of young endosperm, *E*, and the shrunken protoplasmic lining, *L*, of the residual cavity. × 52.

FIG. 31. Longitudinal section of a swollen embryo-sac surrounded by the inner integument. *A*, the egg cell with the nucleus just divided, *E*, the endosperm, *R*, residual nucleus in the greatly enlarged cavity. × 52.

FIG. 32. Residual nucleus shown in FIG. 31. × 160.

FIG. 33. Longitudinal section of mature ovary, showing the stigmatic hairs at outer and inner end of style and the slime, *s*, in the cavity. × 15.

PLATE 3

FIGS. 34–38. Stages in the opening of a plumule leaf. × ⅔.

FIG. 39. A normal first year leaf. × ⅔.

FIGS. 40–42. Opening of second year leaf. 40, × ½; 41 and 42, × 1.

FIG. 43. A three-lobed first year leaf. × ⅔.

FIGS. 44, 46, 52. Unfolding of leaves of mature plants. × ¼.

FIG. 47. A plant bearing two flower clusters. × ⅛.

FIG. 48. Diagrammatic section of corm, showing terminal bud, *B*, lateral bud, *LB*, and starch mass, *S*, to be absorbed during the season.

FIG. 49. Third year corm. × 2.

FIGS. 50, 51. Mature corms drawn out of a vertical position by root contraction. × ⅓.

FIGS. 53, 54. Diagrammatic cross section of leaves in buds of mature plants. *S*, scape.

PLATE 4

FIG. 55. A flower spike with almost equal numbers of pistillate and staminate flowers. × 1.

FIG. 56. A bud dissected out of a 90 g. corm, August 14. × 1½.

FIG. 57. A staminate spike with one pistillate flower, *O*, near the base, and probably containing fertilized ovules. × 1.

FIG. 58. A group of average seedlings. × ½.

FIG. 59. A pistillate spike with imperfect staminate flowers on long filame at the top. × 1.

FIG. 60. A staminate spike with scattered pistillate flowers. × 1.

FIGS. 61, 62. Corms at the end of the first growing season. × 1. Most of those in FIG. 61 are probably from blind germinations.

PLATE 5

FIG. 63. Cross section of root tip just above the calyptrogen. *C*, root cap *P*, plerome; *R*, raphide cells. × 70.

FIG. 64. Cross section of root tip about 1 mm. above FIG. 63. Parts lettered as in FIG. 63. × 70.

FIG. 65. A part of a longitudinal section of a root tip showing the beginning of raphide cells, *R*. × 70.

FIG. 66. Cross section of a five-rayed stele. × 60.

FIG. 67. Longitudinal section of a root, showing regional divisions and young raphide cells, *R*. × 35.

FIG. 68. Longitudinal section of a mature, contracted root, showing the folding and twisting of the stele after sectioning. The cells of the sheath, *B*, show no distortion. × 25.

FIG. 69. Mature corm, showing extensive root system and two buds, *B*, which have formed leaves while attached to the parent plant. × ⅓.